

Macroecology of West African Amphibians

Dissertation

zur Erlangung des akademischen Grades
doctor rerum naturalium
(Dr. rer. nat.)
im Fach Biologie

eingereicht an der

Lebenswissenschaftlichen Fakultät
der Humboldt Universität zu Berlin

von

Dipl. Biol. Johannes Penner

Präsident der Humboldt-Universität zu Berlin
Prof. Dr. Jan-Hendrik Olbertz

Dekan der Lebenswissenschaftlichen Fakultät
Prof. Dr. Richard Lucius

Gutachter: 1. PD Dr. Mark-Oliver Rödel
2. Prof. Dr. Johannes Müller
3. Prof. Dr. Liliane Rueß

Tag der mündlichen Prüfung: 30. April 2014



Johannes Penner



Macroecology of West African Amphibians







Theories pass – the frog remains
(Jean Rostand)



To Helena & Petra





Content

1 Abstracts	8
1.1 English abstract	8
1.2 Deutsche Zusammenfassung	9
2 Introduction	10
2.1 Amphibians	10
2.2 Thesis overview	11
3.1 Examples of taxonomic clarifications	14
3.1.1 A new cryptic <i>Phrynobatrachus</i> species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa	14
3.1.2 The taxonomic status of <i>Hyperolius spatzi</i> Ahl, 1931 and <i>Hyperolius nitidulus</i> Peters, 1875 (Amphibia: Anura: Hyperoliidae)	22
3.1.3 The genus <i>Astylosternus</i> in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae)	30
3.2 The uniqueness of West African amphibians	50
3.2.1 A hotspot revisited - a biogeographical analysis of West African amphibians	50
3.3 Threats - the case of the Chytrid fungus	62
3.3.1 West Africa - A safe haven for frogs? A sub-continental assessment of the chytrid fungus (<i>Batrachochytrium dendrobatidis</i>)	62
3.4 Niches of West African amphibians	72
3.4.1 Leaping forward - Providing the spatial baseline for amphibian conservation across West Africa	72
3.4.2 Keep it simple? Dispersal abilities can explain why species ranges differ	88
4 Discussion	96
4.1 General discussion	96
4.2 Outlook	97
5 Acknowledgements	100
6 Bibliography	102
7 Appendices	126
8 List of Publications	162
9 Statement / Erklärung	169



1 Abstracts

1.1 English abstract

Amphibian populations are declining on a global scale. In order to make informed conservation decisions, one needs a sound scientific background on a variety of aspects of amphibian biology. For conservation one major component is the distribution of a species and the underlying causes for the observed patterns. This also requires clarity on the taxonomic status of the analysed species. Often neglected regions in terms of conservation as well as basic knowledge are located in the tropics. In order to fill this gap and provide respective answers, the present thesis examines the macroecology of West African amphibians in four parts.

The opening part deals with selected taxonomic examples. First, a new species of the family Phrynobatrachidae (*Phrynobatrachus intermedius*) is described. Afterwards, the taxonomic differences between morphologically similar members of the families Hyperoliidae, *Hyperolius spatzi* and *H. nitidulus*, and Arthroleptidae, *Astylosternus occidentalis* and *A. laticephalus*, are discussed. Beside other studies, this sets the field for the macroecology parts.

The second part tests whether West Africa is a unique biogeographic region. It analyses the similarity of 120 amphibian assemblages which comprise 528 species from Sub-Saharan Africa. It is shown that West Africa indeed contains unique amphibian assemblages. Similarities between assemblages within the West African region are higher than similarities between the same habitats (forest and savannahs) across different regions. The main barrier towards Central Africa is the Cross River. Furthermore, several geographic divisions within West Africa are detected.

The third part examines whether one major threat to amphibians occurs in the West African region. The chytrid fungus *Batrachochytrium dendrobatidis* is thought to be responsible for amphibian population declines in many regions of the world. Despite a large dataset across 62 species from 64 sites in seven countries, so far there is no positive record west of Nigeria. However, models predict that environmental suitability for this fungus is high. The most plausible explanation for the absence of this fungus is that the Dahomey Gap acted as a natural barrier against the spread of the *Batrachochytrium dendrobatidis* from Central Africa into West Africa.

The fourth part investigates the niches of West African amphibians as defined in the second part. For most species (176 out of 192) environmental niche models are calculated based on environmental parameters from known occurrence records (total n = 15944) and extrapolated into geographic space. This confirms previously known areas of high alpha diversity (e.g., south-eastern Côte d'Ivoire and south-western Ghana). Moreover, so far unknown species rich areas (parts of north-western Liberia) are detected. In a further study, explanations for differing range sizes are searched for. Niche breadth is commonly assumed to be the general cause. However, the analysed data also suggests that a more simple explanation, namely dispersal ability, captured in a simple index, can also explain the observed pattern.

Finally, a discussion and a short outlook summarise the main findings, based on the present work potential future research is shown which could supplement the conducted work by integrating more information on conservation, beta diversity as well as on climate change.

1.2 Deutsche Zusammenfassung

Amphibienpopulationen sind weltweit bedroht. Um fundierte Entscheidungen im Naturschutz zu treffen, ist ein solides wissenschaftliches Hintergrundwissen zur Biologie der Amphibien notwendig. Für den Naturschutz ist die Verbreitung der Arten eine essentielle Komponente, sowie die Gründe, die den beobachteten Mustern zugrunde liegen. Dies setzt auch Klarheit bezüglich des taxonomischen Status der analysierten Art voraus. Regionen, die vom Naturschutz und der Forschung oftmals vernachlässigt werden, liegen meist in den Tropen. Um diese Lücke zu füllen und entsprechende Antworten geben zu können, untersucht die vorliegende Arbeit die Makroökologie westafrikanischer Amphibien in vier Teilen.

Zu Beginn wird die Taxonomie behandelt. Zunächst wird eine neue Art der Familie Phrynobatrachidae (*Phrynobatrachus intermedius*) beschrieben. Anschließend werden die taxonomischen Unterschiede jeweils zweier morphologisch ähnlicher Mitglieder der Familien der Hyperoliidae, *Hyperolius spatzi* und *H. nitidulus* sowie der Arthroleptidae, *Astylosternus occidentalis* und *A. laticephalus*, diskutiert. Neben anderen Arbeiten ebnet dies den Weg für die folgenden makroökologischen Bereiche.

Der zweite Teil analysiert, ob Westafrika eine einzigartige biogeographische Region ist. Die Untersuchung von 120 Amphibiengemeinschaften mit insgesamt aus 528 Arten aus dem Gebiet südlich der Sahara zeigt, dass Westafrika in der Tat einzigartige Amphibiengemeinschaften beherbergt. Die Ähnlichkeiten innerhalb der westafrikanischen Region sind größer als die innerhalb ähnlicher Habitate (Wälder und Savannen) quer durch unterschiedliche Regionen. Der Cross River stellt sich hierbei als die wichtigste Barriere gegenüber Zentralafrika heraus. Des Weiteren werden mehrere geographische Zonierungen innerhalb Westafrikas entdeckt.

Im dritten Abschnitt wird untersucht, ob eine der größten Bedrohungen für Amphibien in der Region Westafrika vorkommt. Der Chytrid Pilz, *Batrachochytrium dendrobatidis*, wird für den Rückgang diverser Amphibienpopulationen in unterschiedlichen Regionen verantwortlich gemacht. Trotz eines großen Datensatzes, der 62 Arten aus 64 Lokalitäten aus sieben Ländern beinhaltet, gibt es bisher keinen positiven Nachweis westlich Nigerias. Dennoch haben Modellierungen geeignete Habitate für diesen Pilz vorhergesagt. Die wahrscheinlichste Erklärung für die Abwesenheit dieses Pilzes ist, dass die Dahomey Gap als natürliche Barriere fungiert und so die Ausbreitung von *B. dendrobatidis* von Zentral- nach Westafrika verhindert.

Das vierte Kapitel eruiert die Nischen westafrikanischer Amphibien. Für die meisten Arten (176 von 192) wird die Nische anhand von Umweltparametern an bekannten Fundorten (Gesamt $n = 15944$) berechnet und in den geographischen Raum extrapoliert. Dies bestätigt bereits bekannte Gebiete mit hoher Alpha Diversität (bspw. der süd-östliche Teil der Elfenbeinküste und der südwestliche Teil Ghanas), zeigt aber auch bisher unbekannte artenreiche Gebiete auf (bspw. Teile des nordwestlichen Liberias). In einer weiteren Untersuchung werden Erklärungen für unterschiedliche Verbreitungsgebietsgrößen gesucht. Generell wird die Nischenbreite der Art hierfür verantwortlich gemacht. Die vorliegenden ausgewerteten Daten lassen allerdings den Schluss zu, dass eine einfachere Erklärungsmöglichkeit, nämlich das Ausbreitungsvermögen einer Art, welches mit einem schlichten Index berechnet werden kann, das beobachtete Muster ebenfalls erklären kann.

Schlussendlich fassen eine Diskussion und ein kurzer Ausblick die wichtigsten Ergebnisse zusammen. Aufbauend auf der vorliegenden Arbeit werden weitere Forschungsmöglichkeiten aufgezeigt, die die bisherige Arbeit ergänzen können, indem sie mehr Informationen mit Bezug auf Naturschutz, Beta Diversität und Klimawandel integrieren.

2 Introduction

Where do species occur and why? These two fundamental questions have puzzled scientists for decades and are important on a number of different levels. They are part of the fundamental question of how many species there are on earth (e.g. Mora *et al.* 2011). It is not sufficient to count species without knowing where they occur (Lomolino *et al.* 2004). Besides taxonomic characters, it can often be the geographic distribution that defines a species. If these distributions of species are known, it is a small step to more complex questions such as ‘Where are unique areas, e.g. centres of endemism?’ or ‘Where are areas of high diversity?’. Ultimately, a logical follow up question is ‘What are the causes for the observed patterns?’. The causes might be grouped into abiotic, biotic and historical/evolutionary factors; quite often they are a combination of these.

These two very broad research themes - where and why species occur - can be summarised as “biogeography” or in the case of animals “zoogeography”. However, besides the pure scientific viewpoint there is another important aspect to biogeography which has become a fast growing field over the last decades, namely the aspect of applied conservation. In an ever changing world where more and more species are facing an increasing threat of extinction, informed decisions on which areas to protect are needed, how to link these protected areas and where to set spatial priorities (e.g. see Moilanen *et al.* 2009; Kukkala & Moilanen 2013). Biogeography plays an important role by identifying unique regions due to their high number of co-occurring species and/or their high number of evolutionary unique species and/or their number of endemic species. Complementarily, “Macroecology is a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution and diversity” (Brown 1995). In other words, it is the study of the mechanisms behind the distribution of species and the relationship between species and their environment on a large scale (see Brown & Maurer 1989; Brown 1995). Nevertheless, the terms biogeography and macroecology refer to similar research agendas and it is subject to debate whether they are interchangeable or not.

Since the appearance of Brown’s landmark publication in 1995, both fields have advanced and expanded rapidly. This is due to an increasing availability of data and computing power which makes large scale calculations feasible. Besides many important advances in statistical analyses and implementations, one tool which has had a strong impact on biogeography and macroecology is and will certainly continue to be “Environmental Niche Modelling” (ENM). ENM uses data gathered at points of occurrences of species to calculate their environmental niche in geographic space (e.g. see Franklin 2009; Peterson *et al.* 2011). A number of these algorithms can be used relatively conveniently in a Geographic Information System (GIS) setting and even do not need real absence data which is often difficult to collect.

2.1 Amphibians

The main focus of conservation has shifted since the first “Earth Summit” in 1992 and the ratification of the “Convention of Biological Diversity” (see CBD 2013) from species oriented efforts to ecosystem and biodiversity oriented approaches. In general, biodiversity is globally threatened and declining (CBD 2013). Unfortunately amphibian diversity is not only part of that decline but at the forefront. It is estimated that between 31% to 56% of all amphibian species (currently there are 7044 species assessed) have to be listed as threatened by the IUCN Red List; meaning they are classified as “Critically Endangered”, “Endangered” or “Vulnerable”. This is much higher than the percentages of threatened mammal (21%-36%) or bird species (13%-14%) (IUCN 2013).

A number of causes have been identified to be responsible for the so called “amphibian decline” (Stuart *et al.* 2004). Overall, the number one factor is the destruction and alteration of natural habitats, pollution is ranked second (IUCN 2008). Therefore, it is vitally important for the conservation of amphibian diversity to identify biogeographically important areas and to understand the underlying reasons for these distribution patterns.



A major landmark in the conservation of global amphibian diversity is presented in the “global amphibian assessment”. Experts estimated the distributional ranges for all amphibian species, resulting in a global map of amphibian diversity and identifying mainly ecophysiological constraints at a coarse resolution (Buckley & Jetz 2007; Stuart *et al.* 2008). Overall, Africa still remains something like a dark spot for finer, continental analysis. Most continental results come from global studies and were conducted on a rather large spatial scale (e.g. 0.5°). Nevertheless, first continental and regional efforts were initiated by John C. Poynton and Arne Schiøtz. Poynton concentrated on East and South African and Schiøtz on Central and West African patterns (Poynton 1962, 1999; Poynton *et al.* 2007; Schiøtz 1967).

2.2 Thesis overview

Following up on the work of Schiøtz (1967), distribution patterns of amphibians on a regional scale (West Africa), including the possible reasons behind these patterns, are examined in the present thesis by using modern biogeographical and macroecological tools. The aim is to analyse the current situation of a highly threatened group for which information on distribution and its causes are urgently needed. The approach and research design are explained in the following.

First of all, the approach needs a clear taxonomic base. Ecological analyses are meaningless without at least some degree of certainty of the species' statuses (e.g. see Krell 2004). For amphibians, the field has been well set by a number of scientists working in the African realm. Past and still on-going work in West Africa by Mark-Oliver Rödel and his working group cleared many issues over the last 20 years. Three recent examples are summarised in chapter 3.1. This includes the description of a new cryptic species of Puddle frog (Phrynobatrachidae) in chapter 3.1.1. This diverse group of leaf litter frogs is also commonly used for investigating the effects of habitat alterations (Ernst & Rödel 2005; Ernst *et al.* 2006, 2008; Hillers *et al.* 2008) and to derive the natural history of the region with respect to past climates and Pleistocene refugia in particular (Hillers 2008). Chapter 3.1.2 verifies the status of two medium-sized savannah Reed frogs (*Hyperolius*, Hyperoliidae) and 3.1.3 of two large, ground-dwelling Night frogs (*Astylosternus*, Arthroleptidae).

After this excursion into recent taxonomic changes, the geographic region analysed herein is defined. Looking at a variety of different proposed zonations of Africa (e.g. Udvardy 1975; White 1983; Myers *et al.* 2000; Olson 2001; Burgess *et al.* 2004) which were derived from a variety of continental or global distribution patterns of plants, animals or both, it is evident that there is no clearly defined West African region. Delineations vary quite substantially. Therefore, chapter 3.2 examines how the region West Africa and its delineations can be deduced from amphibian assemblages.

Following that, the question of how threats to amphibians influence the West African region is answered. Despite the fact that habitat destruction, fragmentation and alteration are the most important reasons for the currently observed amphibian decline, a number of other causes are also relevant (IUCN 2008). Frequently discussed is the chytrid fungus *Batrachochytrium dendrobatidis* (Bd). The search for it and its threat to West African amphibians is discussed in chapter 3.3. A large number of collected samples throughout the region is analysed and compared to the findings of a fine grained continental ENM.

There is still a need for more fine grained information on the distribution of amphibian species. Large scale surveys throughout the region are, however, impossible to conduct in order to close all distributional gaps. One extrapolation method of choice is statistical modelling. In chapter 3.4.1 ENM is used for the majority of the known amphibian species and the resulting modelled alpha diversity for the whole region is analysed. The fine grained patterns do also have important conservation implications. Although the ENMs applied in 3.4.1 calculate an environmental niche based on 18 environmental parameters, there are still a number of important other niche parameters which are not considered in this approach. Consequently, chapter 3.4.2 adds additional information on the niches of West African amphibians, which



could not be used in geographical space and investigates whether the cause for species range sizes can be found in dispersal abilities.

Finally a short outlook is given of potential future research which should be conducted with the collected data sets and could be used to supplement the results already gained.





3.1 Examples of taxonomic clarifications

In general, the taxonomy of West African amphibians is well resolved. Currently 192 species and candidate taxa (see Vieites *et al.* 2009) are recognised which belong to two orders totalling to 15 families (Anura: 13 families; Gymnophiona: 2 families). Herein, three taxonomic treatments are given.

3.1.1 A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa

3.1.1.1 In a nutshell



A new medium-sized *Phrynobatrachus* species from primary forest in south-western Ghana is described. *Phrynobatrachus intermedius* sp. nov. exhibits a combination of unique morphological and colour characters including: compact body, short and pointed snout, a conspicuous dark face mask that covers the loreal and the tympanal area, a relatively smooth dorsum with only very feebly developed dorsal ridges, a black throat with few small white spots, a breast with blackish vermiculation, and moderately developed webbing. Furthermore, the analysis of mitochondrial 16S rRNA revealed that this new species differs from other West African species of the genus by a minimum distance of 3.4%. The new species is morphologically most similar to *P. liberiensis* (genetic distance 3.4–5.8 %) and *P. plicatus* (> 10% difference in the 16S rRNA fragment examined). *P. liberiensis* from the type locality of the new species are genetically more distant to the new species than those from other West African localities.

3.1.1.2 Introduction

The genus *Phrynobatrachus* Günther, 1862, family Phrynobatrachidae Laurent, 1941, currently comprises 77 species and is endemic to savannahs and forests in sub-Saharan Africa (Poynton 1999; IUCN *et al.* 2004; Frost 2007; Uyeda *et al.* 2007; Hillers *et al.* 2008a). Eighteen valid species are recognized to occur in West Africa west of the Dahomey Gap, the majority living in forest habitats (Guibé & Lamotte 1963; Perret 1988; Rödel & Ernst 2002b; Rödel *et al.* 2005a). The Global Amphibian Assessment database lists 15 Ghanaian *Phrynobatrachus* species (IUCN *et al.* 2004). However, *P. albolabris* (Ahl, 1925 “1924”) and *P. vogti* Ahl, 1924 seem to be conspecific with *P. accraensis* (Ahl, 1925 “1923”) (types examined by M.-O. Rödel, unpublished data), as is *P. latifrons* Ahl, 1924 (Rödel & Agyei 2003). In addition, the record of the Central African *P. batesii* (Boulenger, 1906) is most likely based on a misidentification. Hence, 12 *Phrynobatrachus* species are currently known to occur in Ghana (Schlötter 1964; Hughes 1988; Rödel & Agyei 2003; Rödel *et al.* 2005b; Leaché *et al.* 2006). During a recent survey in the southern Ghanaian forests (Hillers *et al.* 2009 in press) we detected a forest *Phrynobatrachus* that, in the field, was tentatively assigned to *P. liberiensis* Barbour & Loveridge, 1927. However, subsequent morphological and genetic analyses revealed that it represents an unknown species that we describe herein.

3.1.1.3 Material and methods

Measurements were taken by one person (MOR) with a dial calliper (± 0.1 mm) and a dissecting microscope (Leica MZ 95). We recorded snout-urostyle-length (SUL), head width measured directly behind the eyes (HW), femur length (FL), tibia length (TL), foot length including longest toe (FTL), horizontal eye-diameter (ED), horizontal tympanum diameter (TD), inter-orbital distance (IOD), distance from anterior corner of the eye to nostril (EN) and distance from anterior corner of the eye to the snout-tip (ES); webbing formulae [example: 2 (1–2) = second toe (webbing reaches tarsal tubercle number 1 at the interior and number 2 on the exterior side of second toe), tarsal tubercles counted from tip of toe towards toe base; see Rödel 2000], relative toe and finger length, structure of the dorsal and ventral skin, and colour pattern. Sex of

type material was determined through dissection. For comparative material investigated see app. 3.1.1-1, Rödel & Ernst (2002b) and Hillers *et al.* (2008a, 2009 in press). The geographic position of the type locality was collected with a handheld GPS receiver (Garmin 12XL).

We analysed approximately 560 base pairs (bp) of mitochondrial 16S ribosomal RNA from 16 West African *Phrynobatrachus* species (tab. 3.1.1-1, app. 3.1.1-1). DNA was extracted using either QIAamp or DNeasy tissue extraction kits (Qiagen) or High Pure PCR Template Preparation kits (Roche). We used the primers 16SAL and 16SB-H of Palumbi *et al.* (1991) to amplify the 16S rRNA gene. Standard PCR protocols were used and PCR products were purified using QIAquick purification kits (Qiagen) or High Pure PCR Product Purification kits (Roche). Purified templates were directly sequenced using an automated sequencer (ABI 377 or ABI 3100). Sequences were validated using SEQUENCE NAVIGATOR (Applied Biosystems), aligned using the Clustal option in MEGA 4 and refined by eye. Uncorrected pairwise sequence divergence was calculated using PAUP* 4beta10 (Swofford 2002).

Tab. 3.1.1-1: Morphometric measures of *Phrynobatrachus intermedius* sp. nov., *P. liberiensis* and *P. plicatus*. Given are range (minimum to maximum), mean and standard deviation ($\bar{x} \pm \text{sd}$) values; only adult specimens included. For abbreviations see app. 3.1.1-3. For vouchers' data see app. 3.1.1-1.

Species	SUL	HW	FL	TL	FTL
<i>P. intermedius</i> sp. nov. (♀, N=2)	22.81-27.76 25.29±3.5	7.25-9.80 8.52±1.80	13.27-13.77 13.52±0.35	13.37-15.99 14.68±1.85	18.46-23.02 20.74±3.22
<i>P. liberiensis</i> (♀, N=12)	25.69-35.00 31.45±2.87	8.15-11.96 10.14±1.01	12.29-17.94 15.86±1.80	13.91-19.10 17.48±1.54	22.20-27.76 25.01±1.54
<i>P. liberiensis</i> (♂, N=3)	22.31-25.16 23.7±1.43	7.01-8.99 8.05±0.99	11.50-13.91 12.80±1.22	12.54-14.64 13.54±1.50	19.15-20.03 19.51±0.46
<i>P. plicatus</i> (♀, N=8)	28.68-38.59 35.12±3.73	7.25-10.64 9.68±1.15	15.23-19.54 17.81±1.52	17.67-23.20 21.15±1.91	24.20-31.34 28.66±2.77
<i>P. plicatus</i> (♂, N=7)	31.32-40.09 33.71±3.02	8.38-10.47 9.39±0.80	16.83-19.11 17.94±1.01	19.56-22.34 20.89±0.86	25.57-31.04 28.41±2.02
	ED	TD	IOD	EN	ES
<i>P. intermedius</i> sp. nov. (♀, N=2)	2.73-3.28 3.01±0.39	1.34-2.08 1.71±0.52	1.65-2.00 1.83±0.25	1.88-2.44 2.16±0.40	3.49-4.55 4.02±0.75
<i>P. liberiensis</i> (♀, N=12)	31.13-4.53 3.94±0.41	1.85-3.23 2.54±0.40	2.25-3.93 3.11±0.42	2.10-2.97 2.50±0.29	3.40-4.97 4.38±0.52
<i>P. liberiensis</i> (♂, N=3)	2.94-3.51 3.25±0.29	1.53-1.95 1.81±0.24	2.19-2.32 2.27±0.07	1.84-2.19 2.01±0.18	3.07-4.13 3.75±0.59
<i>P. plicatus</i> (♀, N=8)	2.73-4.62 4.06±0.64	1.85-2.86 2.38±0.39	2.93-4.24 3.61±0.49	2.54-3.21 2.85±0.23	4.19-5.47 4.94±0.42
<i>P. plicatus</i> (♂, N=7)	3.57-4.25 3.87±0.25	1.85-2.65 2.45±0.28	3.10-4.50 3.53±0.48	1.91-3.20 2.57±0.46	3.86-5.08 4.52±0.46

3.1.1.4 Results

Phrynobatrachus intermedius sp. nov. (figs. 3.1.1-1 to 3.1.1-4)

Holotype: ZMB 71538 (GB: FJ415751, field and tissue #: MOR ANK28), adult female, primary forest near stream, partly swampy, Ankasa Conservation Area, N 5°16.642', W 02°38.253', Ghana, 2 April 2007, coll. C.O. Boateng & A. Hillers.

Paratype: ZMB 71539 (GB: FJ415752, field and tissue #: MOR ANK30), subadult female, other data as holotype.



Fig. 3.1.1-1: Lateral portrait of a) *Phrynobatrachus intermedius* sp. nov. (ZMB 71538, holotype, female), b) *Phrynobatrachus liberiensis* (ZMB 70728, female), c) *Phrynobatrachus plicatus* (ZMB 71206, male).

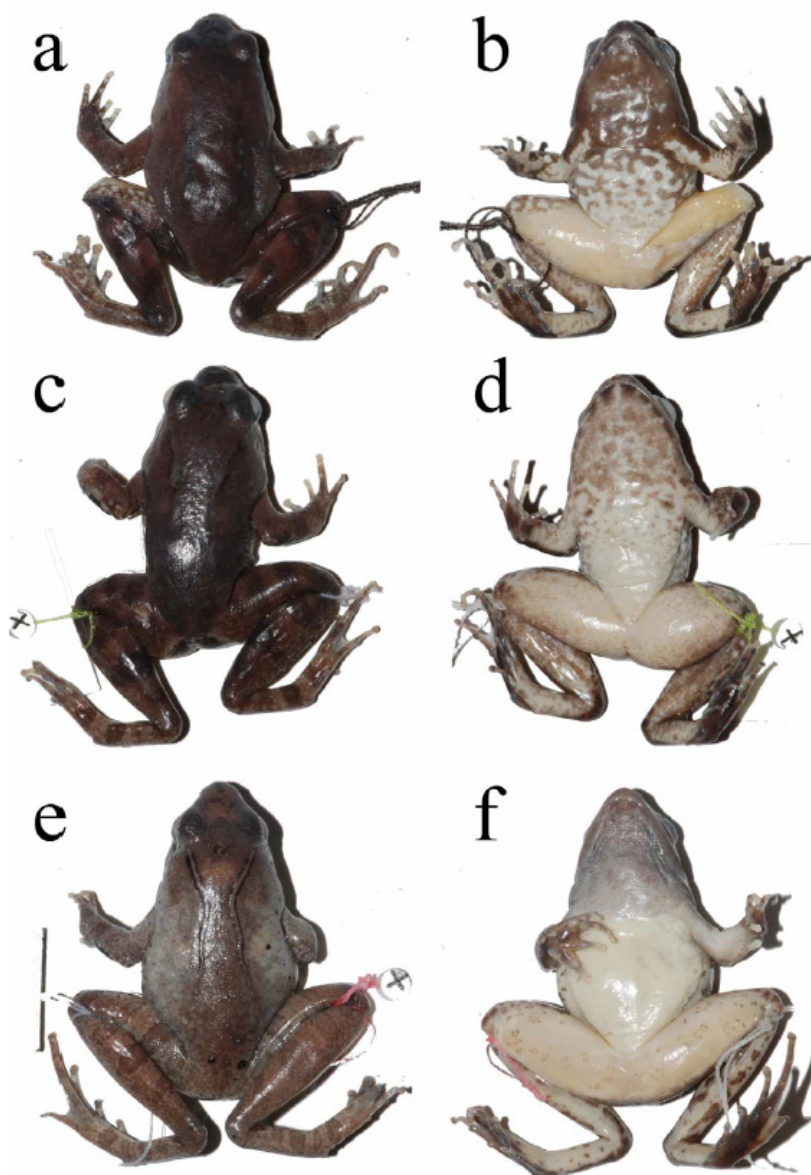


Fig. 3.1.1-2: Dorsal and ventral view of *Phrynobatrachus intermedius* sp. nov. (a, b; ZMB 71538, holotype, female), *Phrynobatrachus liberiensis* (c, d; ZMB 70728, female), *Phrynobatrachus plicatus* (e, f; ZMB 71206, male).

Additional material:

ZMB 71540, juvenile, swampy area with slow moving streams, Nini-Suhien National Park, N 05°17.845', W 02°36', spring 2008, coll. C.O. Boateng.

Diagnosis:

The genetic results show that the new species belongs to the genus *Phrynobatrachus*. Morphologically this is visible by the body shape; presence of tarsal tubercle; presence of inner and outer metatarsal tubercle; presence of feebly developed, slightly converging dorsal ridges; lack of parallel dorsal ridges; lack of black spot in the tympanal region; lack of fine medial dorsal skin raphe; neither finger nor toe tips heart shaped nor expanded to discs.

Medium-sized, compact *Phrynobatrachus*, characterized by combination of comparatively smooth back with feebly developed dorsal ridges; triangular face mask, consisting of dark loreal and tympanal region; absence of eyelid cornicle; short and pointed snout; blackish throat with a small number of white spots; breast with blackish vermiculation; and well developed webbing.

Description of the holotype (measures in mm):

Adult female with numerous, unripe, small white eggs in the oviducts; typical *Phrynobatrachus* with oval, compact body shape; snout-urostyle-length: 27.76; short snout, rounded in dorsal and pointed in lateral view; canthus rostralis distinct and sharp; loreal region plain; head-width directly behind the eyes: 9.80; eye-diameter: 3.28; distance eye-nostril: 2.44; distance eye-snout tip: 4.55; nostril closer to snout than to eye; tympanum present but indistinct, tympanum diameter: 2.08, smaller than diameter of eye; femur: 13.77, slightly shorter than tibio-fibulare: 15.99; foot including longest toe: 23.02; hand with large, oval palmar and thenar tubercles; fingers with small roundish subarticular tubercles, no additional tubercles on hands; relative finger length: 1=2>4>3; palmar webbing absent; tarsal tubercle present; large and oval internal and smaller, round external metatarsal tubercle; inner metatarsal tubercle approximately one third of shortest toe length; relative toe length: 1<2<5<3<4; webbing formula: 1 (1), 2 (1-0.5), 3 (2-1), 4 (2.5), 5 (1); toe and finger tips slightly expanded without forming discs. Dorsal skin grainy; eyelids smooth; back with inconspicuous dorsal ridges that start behind the eyes on the level of the tympani, converge slightly and end shortly posterior to the bases of the forelegs; no other warts discernible; ventral skin smooth.

Overall colouration of the dorsum reddish-brown, slightly fading towards the belly to a greyish-brown; small bluish spots in the middle of the back, positioned on both sides in line with the dorsal ridges; dorsal parts of forelegs without blackish bars; femur and tibia dorsally with three indistinct dark bars; outer, posterior parts of thighs uniform reddish-brown; anterior part of thighs lighter and slightly mottled with brown; vent in the middle of black triangle that is dorsally bordered by fine white line; very conspicuous dark chocolate brown to blackish triangular face mask, starting at snout tip and covering loreal and tympanal region; dorsally this mask bordered by fine, irregularly bordered white line; posterior to tympanum the face mask curves down to bases of forelegs, following fine supratympanal ridge; upper and lower mandible slightly darker than face mask and throat, with very few minute white points; throat dark brown with irregular

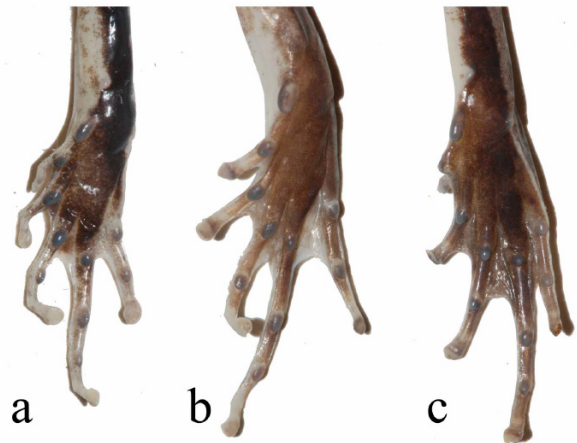


Fig. 3.1.1-3: Hind feet of a) *Phrynobatrachus intermedius* sp. nov. (ZMB 71538, holotype, female), b) *Phrynobatrachus liberiensis* (ZMB 70727, female), c) *Phrynobatrachus plicatus* (ZMB 71206, male).

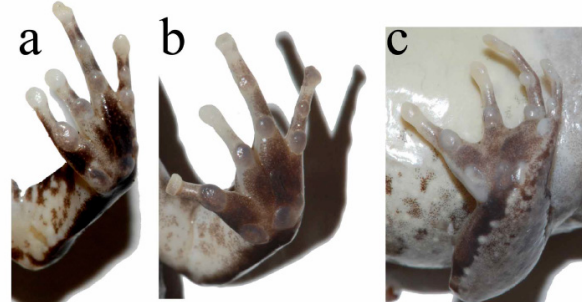


Fig. 3.1.1-4: Hands of a) *Phrynobatrachus intermedius* sp. nov. (ZMB 71538, holotype, female), b) *Phrynobatrachus liberiensis* (ZMB 70728, female), c) *Phrynobatrachus plicatus* (ZMB 71206, male).



white spots; breast and upper part of belly white with dark brown vermiculation pattern; remainder of belly and ventral part of thighs white to beige; dark colour of throat extending to anterior parts of upper arm; lower arm and lower leg with fine darker mottling; colour in preservation slightly faint, otherwise not very different to life; dorsal bluish spots in life green.

Variation:

Further measures and body relations of type material are summarized in tabs. 3.1.1-1 and 3.1.1-2. The non-type specimen differs slightly in the extension of the dark portion of the ventral pattern. The paratype is a subadult female with a uniform brown back, while the juvenile has a clear pair of dorsal spots. Both possess the dark face masks. The paratype has some white spots on the lower arm. Males of this species are so far unknown.

Tab. 3.1.1-2: Morphometric relations of *Phrynobatrachus intermedius* sp. nov., *P. liberiensis* and *P. plicatus*. Given are mean and standard deviation ($\bar{x} \pm \text{sd}$) values; only adult specimens included. For abbreviations see material and methods. For vouchers' data see app. 3.1.1-1.

Species	HW/SUL	FL/SUL	TL/SUL	FTL/SUL
<i>P. intermedius</i> sp. nov. (♀, N=2)	0.34±0.02	0.54±0.06	0.58±0.01	0.82±0.01
<i>P. liberiensis</i> (♀, N=12)	0.32±0.02	0.50±0.04	0.56±0.04	0.80±0.04
<i>P. liberiensis</i> (♂, N=3)	0.34±0.02	0.54±0.02	0.57±0.08	0.82±0.04
<i>P. plicatus</i> (♀, N=8)	0.28±0.03	0.51±0.04	0.61±0.06	0.82±0.07
<i>P. plicatus</i> (♂, N=7)	0.28±0.02	0.53±0.03	0.62±0.03	0.84±0.04

Genetics:

Both *Phrynobatrachus intermedius* types were identical in the 560 investigated base pairs of the 16S rRNA gene. Compared to 16 West African and Central African species of the genus *Phrynobatrachus*, the new species differed by 3.4–16.6% (tab. 3.1.1-3). From the morphologically most similar species, *P. liberiensis* and *P. plicatus*, the new species differed by 4.7 ± 0.7 % (mean \pm standard deviation; N= 15) and 10.9 ± 0.0 % (N= 7), respectively. *P. liberiensis* from the *P. intermedius* type locality, the Ankasa Resource Reserve, were genetically more distant to the new species (5.8 ± 0.0 %, N= 3) than specimens from other parts of West Africa (4.4 ± 0.5 %, N= 12; tab. 3.1.1-3 and app. 3.1.1-1).

Natural History:

All specimens of the new species were collected in swampy parts of primary rainforest in the Ankasa Reserve. This reserve is divided into two: the Ankasa Resource Reserve and the Nini-Suhien National Park, collectively called the Ankasa Conservation Area. The two types have been collected in the swamps of the Resource Reserve, where the new species occurs, amongst other frog species, in sympatry with *P. liberiensis* and *P. plicatus*. The juvenile originates from the National Park where it was collected in a swampy primary forest with slow moving streams. At this site *P. ghanensis* was very abundant. Unfortunately no other data on the natural history of this species are available. For more details concerning Ankasa Reserve see Rödel *et al.* (2005b).

Distribution:

Phrynobatrachus intermedius is only known from two sites in the Ankasa Reserve in southwestern Ghana (fig. 3.1.1-5).

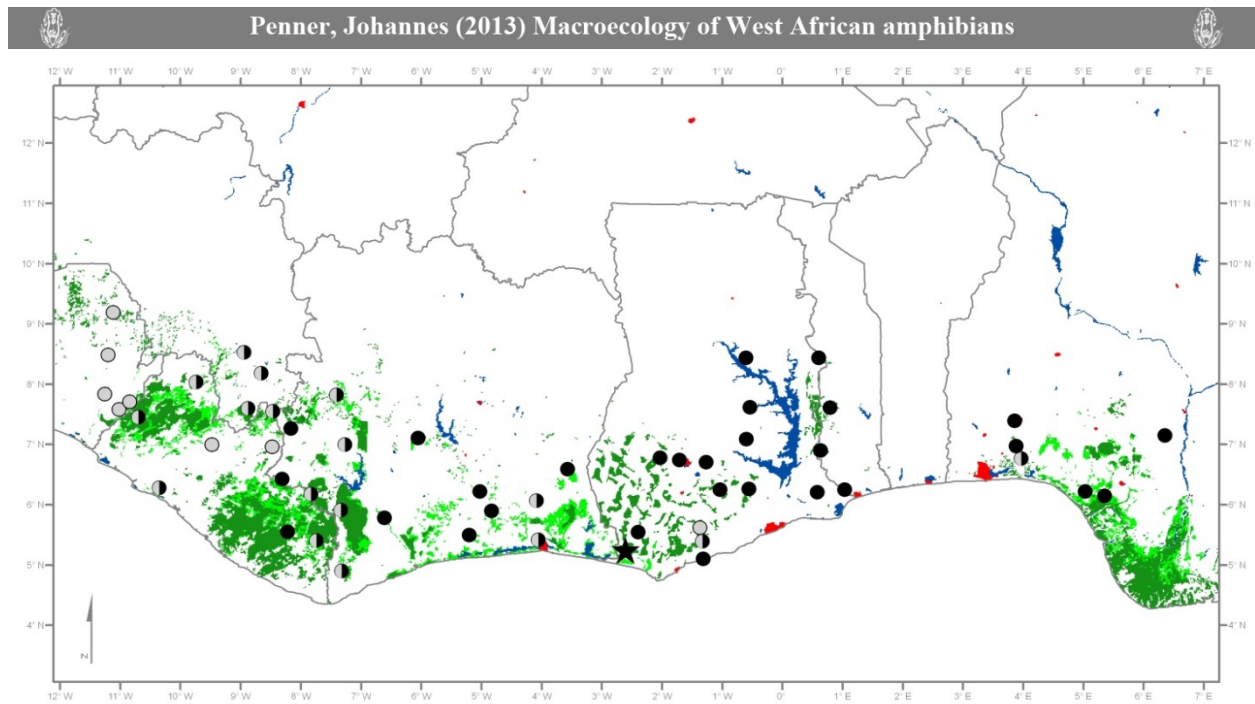


Fig. 3.1.1-5: Distribution of *Phrynobatrachus intermedius* sp. nov. (star), *Phrynobatrachus liberiensis* (grey) and *Phrynobatrachus plicatus* (black). Green areas refer to larger remaining rainforests (dark grey: primary forest; light green: degraded forests). At the type locality *P. intermedius* occurs in sympatry with *P. liberiensis* and *P. plicatus*. Nigerian records of *P. plicatus* and *P. liberiensis* may refer to further undescribed species.

Tab. 3.1.1-3: Genetic distances (uncorrected p) in the mitochondrial 16S ribosomal RNA of 16 *Phrynobatrachus* species, compared to *P. intermedius* sp. nov. (GB: FJ415751 & FJ415752). Given are mean and standard deviation. Data for *P. liberiensis* are also given according to origin, i.e. Ankasa National Park (the type locality of *P. intermedius* sp. nov.) and other localities. For locality data of the tissue vouchers and GenBank accession numbers see app. 3.1.1-1.

<i>Phrynobatrachus</i> species	Mean	SD	N
<i>P.alleni</i>	0.129		1
<i>P.annulatus</i>	0.128		1
<i>P. batesii</i>	0.077		1
<i>P. calcaratus</i>	0.124	0.003	2
<i>P. cornutus</i>	0.166		1
<i>P. fraterculus</i>	0.124		1
<i>P. ghanensis</i>	0.144		1
<i>P. guineensis</i>	0.135		1
<i>P. gutturosus</i>	0.141		1
<i>P. liberiensis</i>	0.047	0.007	15
<i>P. liberiensis</i> (Ankasa Conservation area)	0.058	< 0.001	3
<i>P. liberiensis</i> (not Ankasa Conservation area)	0.044	0.005	12
<i>P. natalensis</i>	0.137		1
<i>P. phyllophilus</i>	0.122		1
<i>P. pintoii</i>	0.145		1
<i>P. plicatus</i>	0.109	< 0.001	7
<i>P. tokba</i>	0.075		1
<i>P. villiersi</i>	0.118		1

Etymology:

The species' name is an adjective chosen because of the unique mixture of morphological similarities of the new species to *P. liberiensis* and *P. plicatus*, making it morphologically intermediate to these two species.

3.1.1.5 Discussion

With a body length longer than 25 mm the new species ranks among the larger West African *Phrynobatrachus*. From a number of the smaller species [*P. annulatus* Perret, 1966; *P. calcaratus* (Peters, 1863); *P. taiensis* Perret, 1988; *P. villiersi* Guibé, 1959] it can be readily distinguished by its size (> 22 mm), the absence of an eyelid cornicle and a different ventral pattern (Perret 1988; Hillers *et al.* 2008). *P. ghanensis* Schiøtz, 1964 and *P. pinto* Hillers, Zimkus & Rödel, 2008a lack an eyelid cornicle, but are also much smaller and have a different ventral colouration. *P. tokba* (Chabanaud, 1921), *P. guttuosus* (Chabanaud, 1921), and *P. fraterculus* (Chabanaud, 1921) are smaller, have a much more slender body shape and differently shaped warts in the neck region (or no warts at all: *P. fraterculus*). These three species have only very rudimentary traces of webbing (Rödel & Bangoura 2004; Rödel & Ernst 2002a; Rödel *et al.* 2005a), whereas *P. intermedius* has a more robust body shape, feebly developed but discernible dorsal ridges and well developed webbing. The ridges differentiate the new species also immediately from *P. brongersmai* Parker, 1936 that has four dorsal warts that form an X-shaped pattern and brown stippling on the gular and pectoral regions (Parker 1936); as well as from *P. guineensis* Guibé & Lamotte, 1961, *P. phyllophilus* Rödel & Ernst, 2002, *P. accraensis* (Ahl, 1925 "1923"), *P. francisci* Boulenger, 1912, and *P. natalensis* (Smith, 1849) that all have warts (mostly two pairs of comma shaped ones) on the neck, but no ridges (Rödel 2000; Rödel & Ernst 2002b). Webbing is also more developed in *P. accraensis*, *P. francisci*, and *P. natalensis* than in the new species. *P. allen* Parker, 1936 has ridges that resemble *P. plicatus* (X-shape, see below) but are shorter. These ridges are also much more distinct in *P. allen* than in *P. intermedius*. Furthermore *P. allen* has either a white (females), or a yellowish (males) venter, whereas the throat and breast are dark coloured in *P. intermedius*. Yellowish throats are also present in males of *P. accraensis* and *P. fraterculus*.

From all *Phrynobatrachus* species previously mentioned, *P. intermedius* differs by the presence of a very distinct blackish-brown face mask, covering the loreal and tympanal region (fig. 3.1.1-

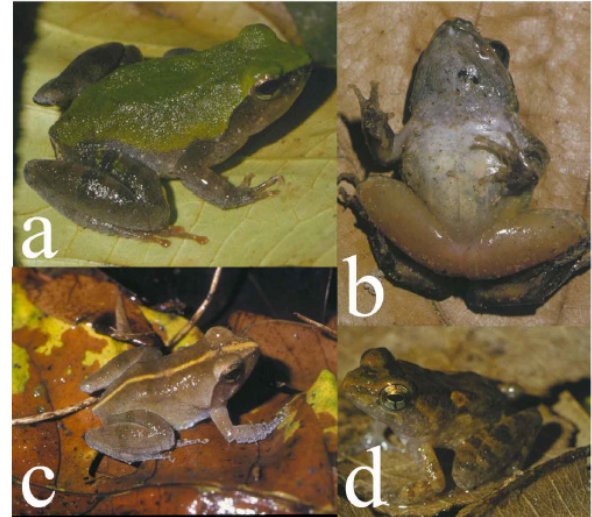


Fig. 3.1.1-6: Variation of *Phrynobatrachus liberiensis*; a) dorsal view with exceptional green color of an adult female; b) ventral view of an adult male; c) semiadult male specimen with vertebral stripe (ZMB 71557); d) typical pattern of juvenile *P. liberiensis* with a symmetrical pair of clear dorsal spots and less conspicuous face mask. All specimens from Taï National Park, Côte d'Ivoire.

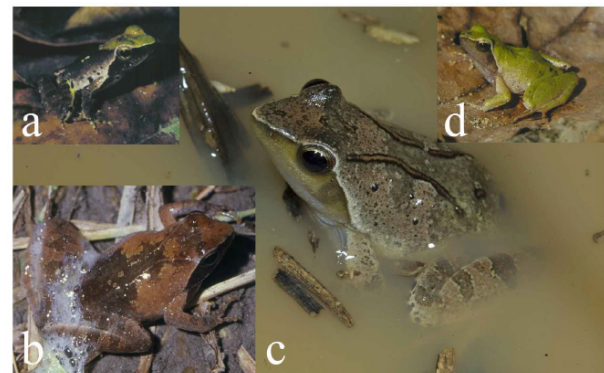


Fig. 3.1.1-7: Variation of *Phrynobatrachus plicatus*; a) rare juvenile pattern with green head and grayish-black back and extremities; b) reddish-brown female with dark dorsal markings shortly after spawning; c) male specimen with typical dorsal pattern of most specimens; d) green adult female. Specimens a, b and d from Taï National Park, Côte d'Ivoire; c from Atewa Range Forest Reserve, Ghana (Photo: P. Naskrecki).

1). Such a face mask is also present in *P. batesii* (Boulenger, 1906), *P. liberiensis* Barbour & Loveridge, 1927 (fig. 3.1.1-6), and *P. plicatus* (Günther, 1858) (fig. 3.1.1-7). The Central African *P. batesii* has much less developed webbing compared to the new species and *P. batesii* females have a white throat (Perret 1966). Thus, *P. intermedius* is morphologically most similar, although somehow intermediate to *P. plicatus* and *P. liberiensis* (figs. 3.1.1-1 and 3.1.1-2). Adult *P. plicatus* and *P. liberiensis* males have very distinct folds on a completely black throat; males of the new species are unknown. *P. intermedius* shares with *P. plicatus* a more pointed snout and a more conspicuous face mask, compared to *P. liberiensis* (fig. 3.1.1-1). In *P. intermedius* the throat bears some small whitish spots or points. Female *P. plicatus* have a uniform dark throat and the *P. plicatus* snout is more rounded in lateral (fig. 3.1.1-1) and more pointed in dorsal view (fig. 3.1.1-2). Both sexes of *P. plicatus* can be readily distinguished from the new species, by having very characteristic, distinct long and X-shaped dorsal ridges that clearly exceed the middle of the back (Lamotte & Xavier 1966). These ridges are usually bordered by a colour that is either lighter or darker than the rest of the back and thus makes the ridges even more conspicuous (figs. 3.1.1-2c, e; 3.1.1-7c). The dorsal ridges are much less conspicuous and shorter in the new species, not exceeding the middle of the back (fig. 3.1.1-2). Few *P. plicatus*, some sympatric with *P. intermedius*, may have comparatively short dorsal ridges (e.g. ZMB 71207, dorsal ridge only reaching middle of the back). However, these are still longer and much more distinct in *P. plicatus* than in the new species, and the ridges converge and diverge, thus forming an X-like figure. *P. intermedius* ridges are only slightly converging. *P. plicatus* further has a less broad head (tab. 3.1.1-2) and more developed webbing than *P. intermedius* (fig. 3.1.1-3, Lamotte & Xavier 1966). The greenish dorsal spots of the *P. intermedius* holotype occasionally occur also in *P. plicatus*. Many *P. plicatus* possess paired or unpaired black spots in the most caudal quarter of the back, a character that we so far could not observe in any other West African *Phrynobatrachus*.

Concerning the investigated part of the 16S rRNA gene, *P. intermedius* is most closely related to *P. liberiensis*. Interestingly *P. intermedius* is less closely related to sympatric individuals of *P. liberiensis*, than to those from other localities, e.g. Côte d'Ivoire, Guinea and Liberia (tab. 3.1.1-3) and thus seems to exhibit a kind of genetic character displacement. Morphologically *P. intermedius* has a similar broad head as *P. liberiensis* (tab. 3.1.1-2), but can be easily differentiated from it by the presence of a more distinct face mask (especially in preserved specimens, where the often conspicuous dark face mask of live *P. liberiensis* fades), a more pointed snout (lateral view, compare fig. 3.1.1-1; the snout is almost round in *P. liberiensis*) and less conspicuous dorsal ridges (figs. 3.1.1-2 and 3.1.1-6). Similar to *P. plicatus*, these ridges are usually bordered black in *P. liberiensis* and further blackish markings that resemble warts may be as well present on the back of this species. Female *P. liberiensis* have very light or even white throats. The juvenile *P. intermedius* has a conspicuous pair of clear dorsal spots, which are also very typical for juvenile *P. liberiensis* (fig. 3.1.1-6), but already possess the very distinct dark face mask.

Currently *P. intermedius* is only known from three specimens (and additional tissue samples where vouchers, due to the suspected conspecificity with *P. liberiensis*, were not collected) and only from its type locality. It hence should be classified as Data Deficient. Future work in southern Ghana and eastern Côte d'Ivoire should very carefully examine *P. liberiensis* and *P. plicatus* to assess if the new species occurs in the few remaining rainforests in this region. However, intensive genetic sampling of many West African forest *Phrynobatrachus* did so far not reveal any further sites (Hillers, unpubl. data). If the species cannot be recorded in further forests it should, because of the size of its range, be classified as Critically Endangered.



3.1.2 The taxonomic status of *Hyperolius spatzi* Ahl, 1931 and *Hyperolius nitidulus* Peters, 1875 (Amphibia: Anura: Hyperoliidae)

3.1.2.1 In a nutshell



We herein re-investigate the taxonomic status of *Hyperolius nitidulus* Peters, 1875 and *H. spatzi* Ahl, 1931 by means of morphology, vocalization and genetic data. Both taxa are morphologically distinct, have different advertisement calls and differ genetically from each other by 5.1–5.6% sequence divergence in the investigated 16S rRNA gene. Based on these data we resurrect *H. spatzi* as a valid species and designate a lectotype for it. Both species occur in savannahs of western Africa. *Hyperolius spatzi* is restricted to Senegambia and thus far known from Senegal and The Gambia. Its occurrence in Guinea Bissau and southern Mauritania seems likely. *Hyperolius nitidulus* ranges from Guinea and Mali eastwards into Nigeria and Cameroon. Records from the driest savannahs in north-eastern Nigerian, Cameroon and the Central African Republic are doubtful and may actually refer to *H. pallidus* Mertens, 1940.

3.1.2.2 Introduction

Many species of the diverse African reedfrog genus *Hyperolius* Rapp, 1842 exhibit very variable colour patterns (Schjøtz 1971, 1975, 1999). Some of these colour variations are age and sex specific (Schjøtz 1967; Veith *et al.* 2009). As these frogs offer comparatively few other species specific morphological characters, this variability caused considerable taxonomic confusion in the past and resulted in the description of many taxa which are now regarded as synonyms (Frost 2010). One author in particular, Ernst Ahl, contributed to this chaos by describing many new species (e.g. Ahl 1931a, b), most of which proved to be invalid (Laurent 1961; Frost 2010). As the in-depth studies of Schjøtz (1967, 1971, 1975) and others have shown, colour and advertisement calls are the most reliable characters for identification of these species. Unfortunately, alcohol preserved *Hyperolius* specimens quickly lose colour (and do not call). Therefore it is often difficult, if not impossible, to evaluate the status of older museum vouchers. Reliable locality data may be of help in some cases where taxa show allopatric distributions and/or different habitat requirements.

One group of savannah dwelling reedfrogs proved to be especially variable and consequently taxonomically complicated: the *Hyperolius marmoratus/viridiflavus* complex (Laurent 1951b, c, 1981; Schjøtz 1971, 1999). These amazing reedfrogs have an outstanding natural history with annual population cycles and spectacular behavioural (Grafe *et al.* 2002), morphological and physiological adaptations, and altogether a unique life history strategy to survive the harsh and long dry seasons (Spieler 1997; Linsenmair 1998; Lampert & Linsenmair 2002 and literature cited therein). So far, they are the only tetrapods where sex change has been documented (Grafe & Linsenmair 1989; for literary use of this knowledge see Crichton 1991). To date, Laurent (1951a, 1976, 1983) and Schjøtz (1971) undertook the most detailed morphological approach to disentangle the nomenclatory chaos of these widespread savannah dwelling frogs, which all share a similar morphology (short snout, very large vocal sac in males, transversal gular fold in females, extensive webbing) and call (xylophone like metallic calls; for summary see Schjøtz 1971, 1999).

However, the mentioned studies of these frogs, using colouration and acoustics, did not provide much insight into their actual taxonomic status (see review by Wieczorek *et al.* 1998). Only more recently Wieczorek & Channing (1997) and Wieczorek *et al.* (2000, 2001) started to apply molecular techniques to disentangle the taxonomic chaos. In the course of their work in particular one member of the *H. viridiflavus*-complex/superspecies/species-group, *H. nitidulus* Peters, 1875, was acknowledged species status, a decision previously already applied for mostly pragmatic reasons by e.g. Schjøtz (1967), Drewes (1984) and Rödel (1996, 2000). This widespread West African savannah frog was described by Peters (1875) from “Yoruba (Lagos)”, Nigeria. It was treated as a synonym of *H. marmoratus* by Boulenger (1882), as a synonym of *H. picturatus* by Loveridge (1955) and as synonym or subspecies of *Hyperolius viridiflavus* by

many other authors (e.g. Laurent 1951a, c, 1961; Schiøtz 1971). The latter author also treated frogs described as *Hyperolius spatzi* Ahl, 1931 from Bakel-Kidira, Senegal (Ahl 1931a, b) as either belonging to *H. nitidulus* (Schiøtz 1967) or as a “subspecies” of *H. viridiflavus* (Schiøtz 1971). In his book, Schiøtz (1999) used the name “spatzi” as a vernacular name, describing “*H. viridiflavus*” populations of uncertain taxonomic status from Senegambia, whereas Rödel (2000) considered *H. spatzi* to represent a junior synonym of *H. nitidulus*. However, already in the late seventies, Böhme (1978) revived the name *H. spatzi* for reedfrogs from Senegal, thus emphasizing their distinctiveness from other West African savannah populations. Recently Emms *et al.* (2006) adopted this view and reported *H. spatzi* from Gambia. Our recent studies of many *Hyperolius* populations at various West African savannah localities are the basis of a taxonomic reinvestigation of both taxa presented herein.

3.1.2.3 Material & methods

Morphological measurements were taken with a dial calliper (± 0.1 mm) and are given in millimetres. Webbing formulae follow the scheme of Rödel (2000). Museum vouchers originated from the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Museum für Naturkunde Berlin (ZMB; app. 3.1.2-2). Calls were recorded with a Sony WM-D6C tape recorder and a directional microphone (Sony ECM-Z157 and Sony ECU-959C9) or an EDIROL R-09 24bit digital recorder (sample rate: 44.1 kHz, record mode: wav_24bit, microphone ECM-950). These calls were analyzed with the program Avisoft SAS Lab Pro 4.5 (R. Specht, Berlin, Germany). For sequence comparisons, we analyzed 247 base pairs (bp) of the mitochondrial 16S ribosomal RNA gene from *Hyperolius spatzi* (ZMB 74280, GenBank HQ113098; Senegal, Sabodala) and *Hyperolius nitidulus* (ZMB 74884, GenBank HQ113099, Sierra Leone, Tingi Hills; no voucher, GenBank HQ113100, Ivory Coast, Mont Sangbé National Park, tissue without voucher). Further hyperoliid gene sequences were obtained from GenBank (tab. 3.1.2-1). DNA extraction, amplification and sequence alignment followed the procedures as described in Rödel *et al.* (2009). Uncorrected pairwise sequence divergence was calculated using PAUP*4b10 (Swofford 2002).

3.1.2.4 Results & discussion

Morphological comparison:

A major problem in using external morphological characters for determination of these frogs is their polymorphism. Schiøtz's (1963, 1967, 1971) described distinct colour phases for many *Hyperolius* species, i.e. called F or A and J or B, respectively. The phase F/A of *H. nitidulus/spatzi* refers to the adult/wet season pattern, whereas phase J/B is the juvenile or sub-adult dry season pattern. Young frogs in dry season condition have a rough, warty dorsal skin which is brown below 35°C and chalk white above this temperature (see figs. in Spieler 1997 and Rödel 2000). Adult frogs have smooth skin and a completely different dorsal colour pattern (fig. 3.1.2-1). These morphological differences are part of the amazing aestivation strategy of these frogs (see Linsenmair 1998; Rödel 2000 and literature cited therein).



Fig. 3.1.2-1: Life coloration of *Hyperolius spatzi* and *H. nitidulus*; upper left: calling *H. spatzi* male from Sabodala, Senegal, remark uniform yellow color at night; lower left: daytime coloration of *H. spatzi* from Sabodala, Senegal, with numerous minute black points; upper right: calling *H. nitidulus* male from Pendjari National Park, northern Benin, remark dark lateral band; lower right: *H. nitidulus* couple from Lamto reserve, Ivory Coast, remark almost uniform yellow color of male and grey mottling on legs and on the flanks in the female.



According to the descriptions by Ahl (1931b) differences between *Hyperolius nitidulus* and *H. spatzi* would be those summarized in tab. 3.1.2-1 (compare also translations of the original descriptions provided in app. 3.1.2-1). Major differences between the descriptions of *H. nitidulus* and *H. spatzi* consist in the fact that the description of the former is based on an adult female, whereas the description of the latter is based on a series of subadult frogs in dry season condition (fig. 3.1.2-2).

Tab. 3.1.2-1: Morphological differences between *Hyperolius nitidulus* and *H. spatzi* based on data provided in the original descriptions and comments based on type specimens and additional material examined herein. Comments which are already deducible from types only, are given in *italic*.

Characters	<i>H. nitidulus</i>	<i>H. spatzi</i>	Comments based on types & additional material
Choanae	large, not hidden beneath edge of mandible	small, hidden below edge of mandible	<i>similar sized & well visible in both species</i>
Tongue	large, broad & heart-shaped	unusually small	<i>tongue in head width spatzi: 3.3 times; nitidulus: 1.7 times</i>
Snout (dorsal view)	roundish pointed	rounded	truncated in dorsal & lateral view in juveniles, a bit more rounded in adults of both taxa
Snout (lateral view)	flattened or roundish truncate	truncated	truncated in dorsal & lateral view in juveniles, a bit more rounded in adults of both taxa
Position of narins	slightly closer to snout-tip than to eye	in mid distance between eye & snout-tip	<i>in both species narins closer to snout-tip than to eye</i>
Position of heels when hind legs arranged to body at right angles	cover or surpass each other	in contact	<i>surpass each other in both taxa</i>
Dorsal skin	skin smooth, laterally smooth or with small warts	thick, almost leathery, rough, beset with many small smooth or rough warts	both taxa with rough skinned juveniles in dry season & smooth skinned adults in wet season
Male gular flap	absent	indistinct	present in both taxa
Dorsal colour	yellow often with dark spots on back	chalk white or fine speckled with dark-brown	<i>H. spatzi</i> with white, brown or yellow back, regularly beset with small black spots; <i>H. nitidulus</i> never with such uniform pattern of black spots
Pattern on flanks	dark canthal & lateral stripe (continuous or broken), bordered white dorsally; below the stripe flanks marbled in dark grey & white	no pattern	in <i>H. spatzi</i> like on back; <i>H. nitidulus</i> with very distinct to rather indistinct lateral b& & dark spots
Body length	28mm	21mm	adults of both species up to about 30mm

Schiøtz (1967, 1971, 1999) mentioned differences between various West African *H. nitidulus* populations, including a cline in pattern from Sierra Leone (few and small spots on flanks) to Cameroon (broad lateral band; same cline in pattern on the lower legs). He also observed an hour-glass pattern and a dark vocal sac in frogs from Sierra Leone (likewise present in some juveniles in northern Ivory Coast, see Rödel 2000). Our specimens from Sierra Leone neither differed in colouration nor in genetics (see below) from e.g. *H. nitidulus* populations from northern Ivory Coast. Schiøtz (1971) further mentions that frogs from drier northern savannahs are more uniform greyish coloured, whereas more southern ones, i.e. from the humid savannah

types, exhibit a distinct pattern. The latter differences might be related to age. Rödel (2000) reported that older specimens are more distinctly coloured. As adult *H. nitidulus* are unable to survive the dry season, all populations are annual (Linsenmair 1998). In more humid savannahs, the wet season lasts longer and frogs may reach older ages (and thus potentially a more colourful pattern).



Fig. 3.1.2-2: Dorsal and ventral views of the types of left: *Hyperolius nitidulus* (ZMB 7729, holotype, adult female) and right: *H. spatzi* (ZMB 32602, lectotype, subadult male).

Almost all anatomical differences (position and size of choanae, position of narins, size, shape, length of extremities, head width) deducible from Ahl's (1931a, b) descriptions (compare tab. 3.1.2-1) are identical among both taxa (for specimens investigated see app. 3.1.2-2). Both species have very short, rounded snouts, females possess a typical gular fold and males have very large vocal sacs with a large but diffuse whitish yellow gular flap (gland). Juveniles are often almost indistinguishable. *Hyperolius nitidulus* juveniles show clear dorsolateral bands or an hourglass pattern shortly after metamorphoses (see figs. in Rödel 2000). In dry season conditions they are uniform brown or white. Juvenile *H. spatzi* in dry season conditions are white with many small black dots, the latter sometimes being indistinct. In contrast, adult frogs are distinctively coloured. The dorsal surfaces of *H. spatzi* are chalk-white to yellow, densely beset with tiny black spots, whereas *H. nitidulus* is brownish or yellowish with black spots and has black lateral lines and spots (plate 18 in Leaché *et al.* 2006). *H. nitidulus* has white, yellow or reddish ventral surfaces, whereas these surfaces are exclusively yellow in *H. spatzi* (see fig. 2f in Emms *et al.* 2006). The hidden

parts of legs are pinkish to blood red in both species (fig. 3.1.2-2 and figs. 430 & 431 in Schiøtz 1999; figs. in Rödel 2000). Generally, females of *H. nitidulus* have a more distinct lateral black pattern than males, which can be

almost uniform brown (fig. 3.1.2-1 and figs. in Rödel 2000). At night, males of both taxa appear uniform yellowish. Usually, the pattern in *H. nitidulus* remains vaguely visible. The only morphological difference detected by us (herein confirming Ahl 1931a, b), is the size and shape of the tongue. *Hyperolius spatzi* usually have comparatively smaller and narrower tongues than *H. nitidulus*, whose tongue is broad and almost heart-shaped. This is also visible in the type specimens of both species.

Acoustics:

The advertisement call of both taxa is a single, pure, metallic and very loud tone (fig. 3.1.2-3). Choruses of both species resemble xylophones or bells. Although superficially similar, advertisement calls of both taxa showed significant differences. The call of *H. spatzi* was of comparatively longer duration and lower frequency (tab. 3.1.2-2). The small sample size and the relatively slight differences in call characteristics urge for some caution in their interpretation. However, the acoustic results are not contradicting the specific distinctiveness of *H. nitidulus* and *H. spatzi*.

Genetics:

The genetic distances in the investigated fragment of the 16S RNA gene between *Hyperolius spatzi* (n = 1) and *H. nitidulus* (n = 3, originating from Sierra Leone and Ivory Coast) ranged from 5.1–5.6%. The mean distance between *H. spatzi* and various other members of the *H. viridiflavus/marmoratus*-complex (N= 33; including *H. nitidulus*) was 5.9% (± 1.1 SD; range: 3.6–8.7%). The lowest distance was present in comparison to a *H. viridiflavus angolensis*, the highest to a *H. viridiflavus viridiflavus* sample (sequences from GenBank, compare tab. 3.1.2-3). Mean genetic distances between *H. spatzi* and nine other *Hyperolius* species was 18.7% (± 3.9

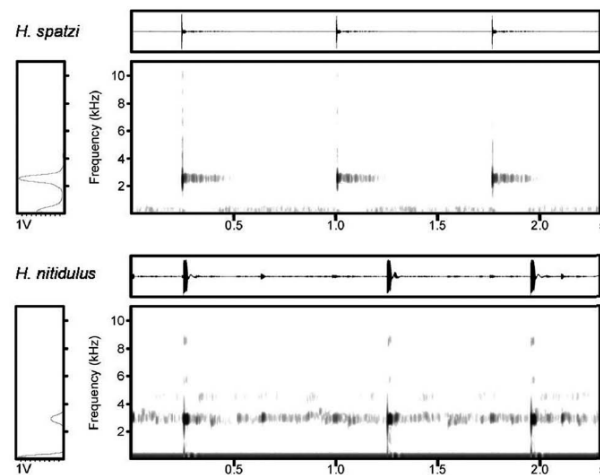


Fig. 3.1.2-3: Waveforms, spectrograms and energy plots of the advertisement calls of *Hyperolius spatzi* (above) and *H. nitidulus* (below; compare tab. 3.1.2-2). The *Hyperolius spatzi* male from Sabodala, Senegal, was recorded in a terrarium. The *Hyperolius nitidulus* was recorded at a savannah pond in Comoé National Park, Ivory Coast. The background noise is a chorus of other *H. nitidulus* males.

sd; range: 11.2–23.2%). The lowest distance present occurred in comparison to *H. fusciventris*, the highest to a *H. cinnamomeoventris* sample (compare tab. 3.1.2-3).

Based on genetic data (12S and 16S), Wieczorek et al. (2000, 2001) recognized *H. nitidulus* as being distinct on the species level from other members of the *H. viridiflavus* group. Altogether they accepted ten species within this group of which *H. nitidulus* was most distinct (within intraspecific genetic variation 0.7–4.8%; between clade variation 2.4–10.0%; Wieczorek et al. 2001). Our data confirm their results and speak in favour of likewise recognising *H. spatzi* as a distinct species.

Distribution:

Hyperolius nitidulus occurs in humid to dry savannahs of West Africa (fig. 3.1.2-4; Lamotte 1966; Schiøtz 1967, 1999; Rödel 2000). Laurent's (1951c) doubts concerning the type locality of *H. nitidulus* were rejected by Schiøtz (1963), by explaining that savannah exists at

the type locality, and thus also suitable habitats for *H. nitidulus*. Records have been published for Benin (Nago et al. 2006), Ghana (Schiøtz 1964a, 1967; Hoogmoed 1980; Hughes 1988; Rödel & Agyei 2003; Leaché 2005; Leaché et al. 2006), Burkina Faso (this paper), eastern and central Guinea (Laurent 1951a, c; Schiøtz 1967; Rödel et al. 2004; Hillers et al. 2006, 2008b; Greenbaum & Carr 2005), Ivory Coast (Laurent 1951c; Lamotte & Perret 1963; Barbault 1967, 1972; Lamotte 1967; Schiøtz 1967; Vuattoux 1968; Euzet et al. 1969; Rödel 1996, 1998, 2000, 2003; Spieler 1997; Linsenmair 1998; Rödel & Spieler 2000; Rödel & Ernst 2003; Adebayo et al. 2010), Mali (Schiøtz 1967), Nigeria (Schiøtz 1963, 1966, 1967; Walker 1968; Onadeko & Rödel 2009), Sierra Leone (Schiøtz 1964b, 1967; Lamotte 1971), and Togo (Bourgat 1979; Segniagbeto et al. 2007).

Hyperolius spatzi, as defined herein, has been recorded from Senegal (Boettger 1881, as *H. cinctiventris*; Loveridge 1956; Schiøtz 1967; Lamotte 1969; Miles et al. 1978, listed as *H. nitidulus*; Ahl 1931a, b; Böhme 1978), and The Gambia (Andersson 1937 as *H. sp.*, but unambiguous description provided; Barnett & Emms 2005 as *H. nitidulus*; Emms et al. 2006). A record from Guinea was actually based on *H. nitidulus* (Hillers et al. 2006; see app. 3.1.2-2). Schiøtz (1971) recognised "*H. viridiflavus spatzi*" as a taxonomic unit occurring in Senegambia and provides a map, indicating the distribution of *H. spatzi* and *H. nitidulus*, respectively (fig. 42 in Schiøtz 1971). Padial & de la Riva (2004) believed that *H. nitidulus* and *H. viridiflavus* may occur in southern Mauritania. *Hyperolius viridiflavus* (sensu stricto) certainly does not occur in western Africa, including Mauritania. *Hyperolius nitidulus* might reach eastern Mauritania and it seems very likely that *H. spatzi* might be a part of the Mauritanian fauna, as is indicated by the close proximity of the type locality of this species to the boarder of Mauritania (fig. 3.1.2-4).

Mountains and rivers can act as potential barriers between taxa (e.g. Li *et al.* 2009, for contrasting results see Gascon *et al.* 1998). In this case, the Géba and Corubal rivers along the border between Guinea-Bissau and Guinea, might fulfil such a role. It is also possible that the northern foothills of the Fouta Djallon serve as an altitudinal barrier. However, more data from Equatorial Guinea, westernmost Guinea, eastern Senegal, western Mali and Mauritania would be needed to clarify the exact limits of the species' ranges.

Tab. 3.1.2-2: Characteristics of the advertisement calls of *Hyperolius spatzi*, recorded in Sabodala, Senegal, and *H. nitidulus*, recorded in the Comoé National Park, Ivory Coast and Mount Nimba, Guinea (fig. 3.1.2-3). Differences of call length, main frequency and time between calls have been tested by comparing mean values of five males of each species (Wilcoxon test).

		Call length [sec.]	Frequency [Hz]	Inter-call intervals [sec.]
<i>H. spatzi</i>	mean	0.08	2638	1.12
	sd	0.04	139.6	0.8
	N (♂)	5	5	5
	N (calls)	25	25	25
<i>H. nitidulus</i>	mean	0.02	2927.6	1.01
	sd	< 0.01	85.1	0.29
	N (♂)	5	5	4
	N (calls)	25	25	20
	W	616	26	218
	P	< 0.0001	< 0.0001	0.4756

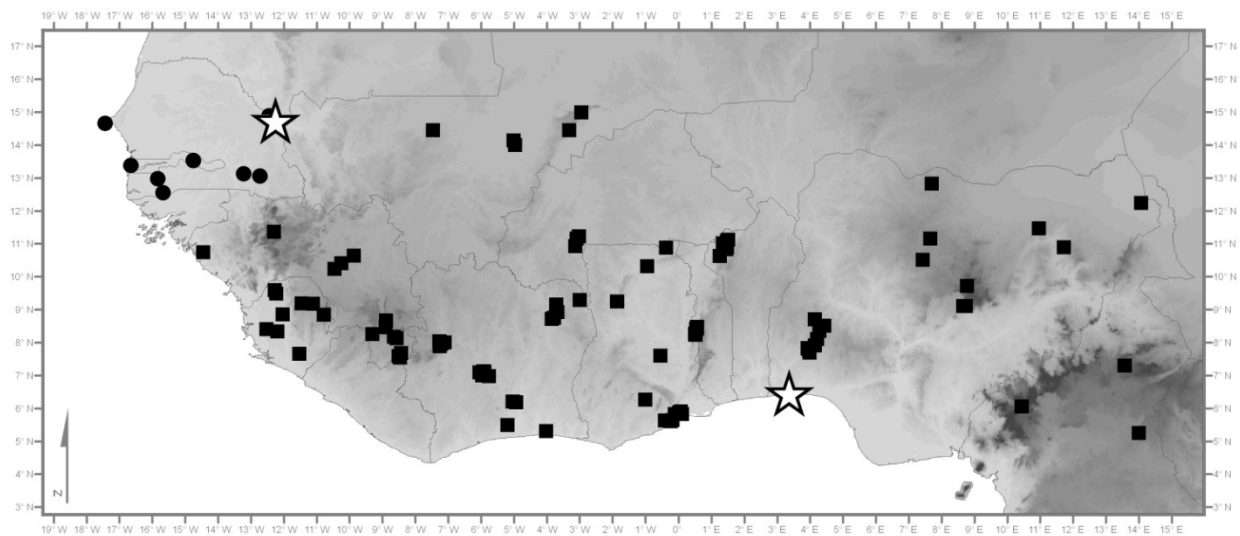


Fig. 3.1.2-4: Known distributions of *Hyperolius spatzi* (circles) and *H. nitidulus* (squares) based on museum and literature records (compare text and app. 3.1.2-2); stars indicate positions of type localities of *H. spatzi* (Senegal) and *H. nitidulus* (Nigeria). The north-westernmost record of *H. nitidulus* in Nigeria may refer to *H. pallidus*, southern and central Cameroonian populations are usually referred to two *H. nitidulus* subspecies (compare text and fig. 428 in Schiøtz 1999).

The distribution of *H. nitidulus* in Central Africa is more complicated. The species is listed as *H. viridiflavus* (subspecies *H. v. nitidulus*, *H. v. pallidus*) for Cameroon, the Central African Republic and the Democratic Republic of Congo by Frétey & Blanc (2000). In northern Cameroon and adjacent north-eastern Nigeria, Chad and the Central African Republic (Joger 1990), *H. nitidulus* may be replaced by *H. pallidus* which was described by Mertens (1940) from dry northern Cameroon (Poli near Garua) and which has been treated by Perret (1966) as a full



species, and by Schiøtz (1971) and Amiet (1973) as a subspecies of *H. nitidulus*. From Cameroonian savannahs, situated a bit further south, two *H. nitidulus* subspecies have been described by Perret (1966). *Hyperolius n. bangwae* occurs in elevated savannahs, i.e. Bamenda, Bamiléké, Adamaoua, whereas *H. n. aureus* is said to occur in the drier northern savannahs and semi-deserts (Perret 1966; compare e.g. Böhme & Schneider 1987 for some records). This view was adopted by Schiøtz (1971) and Amiet (1973). The latter provided arguments for the treatment of these taxa as subspecies of *H. nitidulus*, i.e. Cameroonian frogs differ from typical *H. nitidulus* by slightly smaller size and slightly duller colouration. The voices are “as good as identical” (Amiet 1973). More recently, Amiet thought that all three Cameroonian taxa are subspecies of *H. viridiflavus*, i.e. the highlands of western Cameroon and the Adamaoua plateau being inhabited by *H. v. aureus* (and possibly *H. v. bangwae*), and populations occurring in northern Cameroon (mid-Sudanian, Sudano-Sahelian and Sahelian zones) belong to *H. v. bangwae* and *H. v. pallidus* (J.-L. Amiet pers. comm.).

Tab. 3.1.2-3: Genetic distances between *Hyperolius spatzi* (ZMB 74280; GenBank #: HQ113098) and other *Hyperolius* species. Uncorrected p-distances are based on 247 base pairs of mitochondrial 16S ribosomal RNA. Values for *H. nitidulus* are given in bold.

Genus	Species	"Subspecies"	GenBank #	p-Distance
<i>Hyperolius</i>	<i>chlorosteus</i>		FJ594076	0.214
<i>Hyperolius</i>	<i>cinnamomeoventris</i>		FJ594077	0.232
<i>Hyperolius</i>	<i>concolor</i>		FJ594078	0.203
<i>Hyperolius</i>	<i>fusciventris</i>		FJ594080	0.112
<i>Hyperolius</i>	<i>guttulatus</i>		FJ594082	0.133
<i>Hyperolius</i>	<i>horstocki</i>		AF282410	0.199
<i>Hyperolius</i>	<i>kivuensis</i>		AF282409	0.183
<i>Hyperolius</i>	<i>nasutus</i>		AF215442	0.219
<i>Hyperolius</i>	<i>nitidulus</i>		HQ113099	0.051
<i>Hyperolius</i>	<i>nitidulus</i>		HQ113100	0.051
<i>Hyperolius</i>	<i>nitidulus</i>		AF282435	0.056
<i>Hyperolius</i>	<i>picturatus</i>		FJ594090	0.186
<i>Hyperolius</i>	<i>viridiflavus</i>		AF215440	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>		AF215441	0.061
<i>Hyperolius</i>	<i>viridiflavus</i>		AY323920	0.077
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>angolensis</i>	AF282411	0.036
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>albofasciatus</i>	AF282433	0.065
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>aposematicus</i>	AF282412	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>argentovittis</i>	AF282431	0.046
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>bayoni</i>	AF282413	0.082
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>broadleyi</i>	AF282414	0.071
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ferniquei</i>	AF282416	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ferniquei</i>	AY603987	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>glandicolor</i>	AF282417	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>goetzi</i>	AF282418	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>mariae</i>	AF282419	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>mariae</i>	AF282420	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>marginatus</i>	AF282430	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>melanoleucus</i>	AF282432	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pantherinus</i>	AF282425	0.051
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pitmani</i>	AF282426	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>marmoratus</i>	AF282421	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ngorongoro</i>	AF282423	0.066
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>ommatostictus</i>	AF282424	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>pyrrhodictyon</i>	AF282434	0.046
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>rhodesianus</i>	AF282427	0.038



<i>Hyperolius</i>	<i>viridiflavus</i>	<i>rubripes</i>	AF282436	0.062
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>swynnertoni</i>	AF282415	0.071
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>taeniatus</i>	AF282422	0.056
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>verrucosus</i>	AF282428	0.062
<i>Hyperolius</i>	<i>viridiflavus</i>	<i>viridiflavus</i>	AF282429	0.087

Conclusions:

Our investigations on the type specimens, as well as on additional vouchers, revealed small but distinct morphological (mostly colour pattern; tongue shape and size), significant acoustic and large genetic differences (16S gene). Especially the genetic differences are clearly within the range that is thought to be species specific in anurans (Vences *et al.* 2005a, b; Rödel *et al.* 2009; Vieites *et al.* 2009). Our results thus speak in favour of recognizing both taxa as distinct species. A contradicting argument was seen in the very complicated situation of a large variation of colour patterns between and within populations of the *Hyperolius viridiflavus/marmoratus* species group(s). Schiøtz (1999) thus questions an approach where the taxonomy for only a small part of the continent would be resolved. However, in West Africa it is possible to assign these frogs to particular names and we thus do not see a reason for avoiding it. We therefore herein resurrect the species status of *H. spatzi*, designate a lectotype from the series of syntypes and redescribe the species based on type and new material.

3.1.2.5 Rediscription of *Hyperolius spatzi* Ahl, 1931.

ZMB 32602 (lectotype; fig. 3.1.2-2), 74853-74876 (paralectotypes, formerly all ZMB 32602), all from Bakel-Kidira, Senegal, coll. Spatz.

Description of lectotype (all measurements in mm):

Subadult frog (male, vocal sac barely developed?); short, compact body; snout-vent length 19.2; head width 7.3, head length 6.9, thus head wider than long; snout short and truncated in dorsal and lateral view; narins angular narrow slit, closer to snout-tip than to eye; tympanum hidden; transversal gular fold; tongue small, narrow, almost parallel and notched anteriorly, tongue width 2.3, tongue length 3.2, tongue 3.3 times in head width; choanae small and round, close to edge of mandible but well visible; dorsal skin slightly granular; belly granular (medially dissected); ventral skin on thighs near vent granular, remaining ventral parts of hind limbs smooth; finger and toe tips enlarged to discs; relative lengths of fingers: 1<2<4<3; basal webbing between fingers; femur length: 8.4; tibia length: 10.4; foot incl. longest toe: 14.0; relative lengths of toes: 1<2<3<5<4; webbing formula: 1 (0), 2 (1.5–0), 3 (1.5–0.5), 4 (1–0), 5 (0); subarticular tubercles on fingers and toes not very prominent. Dorsal surfaces chalk white, densely beset with minute black points; ventral skin on thighs near vent white, remaining parts of thighs and ventral parts of shanks, feet, inner parts of forelimbs, ventral part of hands and fingers fleshy coloured.

Variation:

Series of paralectotypes almost indistinguishable from lectotype, exclusively subadult frogs in dry season conditions; dorsal skin partly more or less granular than in lectotype; black points on white ground sometimes more distinct or sometimes almost absent. Further material (see app. 3.1.2-2) exhibit the following variation: Male snout-vent length: 27.0–31.3 (N= 6); female snout-vent length 30.6 (N= 1); snout shape of adult frogs in dorsal and ventral view slightly more rounded than in juveniles; adults of both sexes in ethanol with dorsal surfaces (incl. upper side of thighs) with brownish ground colour (composed of small, very dense brownish points), many very distinct black spots; black spots sometimes a bit more abundant on flanks than on back; some specimens with black spots on throat; others with uniform clear ventral surfaces; tongue in almost all specimens small and comparatively narrow (exception: ZMB 74279). Adult animals in life brownish to yellow with very distinct black spots. These may be not visible during night. Venter yellow.

3.1.3 The genus *Astylosternus* in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae)

3.1.3.1 In a nutshell



Astylosternus laticephalus sp. nov. Rödel, Hillers, Leaché, Kouamé, Ofori-Boateng, Diaz & Sandberger is described from eastern Ivory Coast and western and central Ghana, and compared to *Astylosternus occidentalis* Parker, 1931 from the western part of the Upper Guinea forest zone (western Ivory Coast, Liberia, Guinea and Sierra Leone). Based on a comprehensive sample, including specimens from the entire range, the latter species is re-described. The new species is characterized by a body shape typical for frogs of the genus *Astylosternus*, but has an exceptionally broad head, i.e. broader than in *A. occidentalis*. The basic dorsal pattern of *A. laticephalus* sp. nov. consists of a brownish to brownish red colouration with distinct red dots (red dots are only rarely present in *A. occidentalis*). The new species has bicoloured eyes with the lower part of the iris being grey, the upper third of the iris is orange to red (*A. occidentalis* always has a uniform greyish iris). Males of the new species lack spines on the throat, belly (always present in *A. occidentalis* males), and a layer of black nuptial skin in the pectoral region (present in male *A. occidentalis* from western Guinea). *Astylosternus laticephalus* sp. nov. differs from *A. occidentalis* by a mean pairwise genetic distance of 3.2% in the investigated part of the mitochondrial 16S rRNA gene. Genetic divergence to the morphologically most similar Central African species, *A. diadematus*, was 11.9%. We briefly discuss the phylogenetic position of West African *Astylosternus*, hint on the possibility that the genus might be paraphyletic and discuss the biogeography of West African *Astylosternus*, in particular with respect to forest cover fluctuations in the past.

3.1.3.2 Introduction

The frog genus *Astylosternus* Werner, 1898 currently comprises 11 species (Frost 2010), most of which are endemic to western Central Africa, namely Cameroon (Frétey & Blanc 2000). Frost *et al.* (2006) provide a summary of the history of systematic placements of the genus. We herein follow Frost *et al.* (2006) in treating *Astylosternus* species as members of the family Arthroleptidae. The Central African species have been thoroughly revised by Amiet (1977) and most of them seem to be patchily distributed, often restricted to particular altitudinal zones of mountains or mountain ranges (Mertens 1938; Oates *et al.* 2004; Plath *et al.* 2004; Herrmann *et al.* 2005). Two more widespread Central African species, *A. batesi* (Boulenger, 1900) and *A. diadematus* Werner, 1898, occur in lower to mid-altitudes, south and north of the Sanaga River, respectively (Amiet 1989). Further undescribed species may still occur in western Cameroon (Lawson 1993; Herrmann *et al.* 2006). All *Astylosternus* are forest dwelling leaf-litter frogs and usually occur close to streams, where they attach their egg clutches on stones in partly deeper water. They have large torrenticolous tadpoles with long, muscular tails and characteristic massive mouth parts (e.g. Angel 1930; Mertens 1938; Lamotte & Zuber-Vogeli 1954; Perret 1966).

In the Upper Guinea forests of West Africa only one species, *Astylosternus occidentalis* Parker, 1931 is currently recognised as being valid. This species was described from Sandaru in eastern Sierra Leone and subsequently recorded from a few other sites in the western part of the Upper Guinea forest zone, e.g. the Nimba mountains in Guinea, Liberia and Ivory Coast (Guibé & Lamotte 1958) and the Taï and Haute Dodo forests in Ivory Coast (Rödel & Branch 2002; Ernst & Rödel 2006). Its tadpole was described previously in 1954 but as *A. diadematus* (Lamotte & Zuber-Vogeli 1954). A second species, *Hylambates yalense* Angel, 1944, was described from the Guinean part of the Nimba mountains, but was later regarded as a synonym of *A. diadematus* by Guibé (1950) and of *A. occidentalis* by Lamotte (in Schiøtz 1967). In addition *Astylosternus occidentalis* was listed as occurring in rainforests in Ghana by Hughes (1988).

During the last 15 years we collected *Astylosternus* in forests throughout West Africa. Some of these frogs did not correspond with the typical *A. occidentalis*, i.e. specimens from the Mont



Péko National Park in Ivory Coast (fig. 7 in Rödel & Ernst 2003) and frogs from eastern Ivory Coast and western Ghana (fig. 4 in Rödel *et al.* 2005; Assemanian *et al.* 2006). Based on a large number of individuals from many different West African localities, we investigate the morphology and genetic relationships of these populations, re-describe *A. occidentalis* and describe a new species.

3.1.3.3 Material & Methods

Frogs were sacrificed in a chlorobutanol solution and preserved in 4% formalin or 75% ethanol. Larvae were preserved in 4% formalin. All vouchers are subsequently kept in 75% ethanol. Measurements were taken by one person (MOR) with a dial calliper (± 0.1 mm) and a dissecting microscope (Leica MZ 95). We determined sex, snout-vent length (SVL), head-width at the level of the tympanum (HW), eye diameter (ED), interorbital distance (IOD), internarial distance (IND), distance from the anterior corner of the eye to nose (DEN), distance from nose to snout tip (DNS), horizontal tympanum diameter (TD), length of first finger (LFF), length of second finger (LSF), femur-length (FL), tibia length (TF), foot length incl. longest toe (TFT), length of shortest toe (ST), length of inner metatarsal tubercle (LIM), relative finger and toe length, webbing, colour pattern on head, back, extremities and belly, skin texture on back and secondary sexual male characters such as skin structures and colour of vocal sacs, spines on throat, belly and shanks, as well as nuptial pads. When possible measures were taken on both sides of the body and mean values were used for analyses. Measures are summarised in tabs. 3.1.3-1 and 3.1.3-2. Only adult animals were included in statistical analyses; males and females were compared separately. Description of colour pattern in life is based on photos and field notes. Statistics were calculated with BIAS 8.2-2006 for Windows.

Standard measures and nomenclature of tadpole morphology follows Altig & McDiarmid (1999). The labial-tooth-row formulae are according to Dubois (1995). Staging of tadpoles is according to Gosner (1960). Drawings were done with the aid of a camera lucida. Tadpoles were assigned to the genus *Astylosternus* based on external morphology and to a particular species based on their occurrence and in some cases based on genotyped specimens (*A. occidentalis* only). The geographic positions were either collected with a GPS receiver or geographic positions were taken from The Global Gazetteer (<http://www.fallingrain.com/world>). Coordinates are given as Latitude / Longitude. Material investigated originated from the Muséum National d'Histoire Naturelle Paris (MNHN), the Muséum d'Histoire Naturelle Genève (MHNG), the Museum für Tierkunde Dresden (MTD), the Museum of Vertebrate Zoology at the University of California at Berkeley (MVZ), the Port Elizabeth Museum (PEM), the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Musée Royal de l'Afrique Centrale Tervuren (RGMC), the Zoologisches Forschungsmuseum Alexander Koenig Bonn (ZFMK), the Zoological Museum at the University of Copenhagen (ZMUC), and the Museum für Naturkunde Berlin (ZMB). Further specimens are deposited in national reference collections in the universities of Abobo-Adjamé, Abidjan, Ivory Coast and Kumasi, Ghana. Voucher specimens are listed either at the respective species account (the new species) or in app. 1 (for *A. occidentalis*).

We generated and analysed approximately 536 base pairs (bp) of mitochondrial 16S ribosomal RNA from 29 West African *Astylosternus* (tab. 3.1.3-3 and type series of the new species). For comparisons sequences of three other, Central African, *Astylosternus* and further members of the family Arthroleptidae were obtained from GenBank (tab. 3.1.3-3). DNA was extracted using either QIAamp or DNeasy tissue extraction kits (Qiagen) or High Pure PCR Template Preparation kits (Roche) following the manufacturers protocols. We used the primers 16SA-L and 16SB-H of Palumbi *et al.* (1991) to amplify the 16S rRNA gene. Standard PCR protocols were used and PCR products were purified using QIAquick purification kits (Qiagen), High Pure PCR Product Purification kits (Roche) or NucleoSpin Extract II (Macherey-Nagel). Purified templates were directly sequenced using an automated sequencer (ABI 377 or ABI 3100). Sequences were validated using CodonCode Aligner (version 3.5.7) and Chromas 2.31 (Technelysium Pty Ltd, Helensvale, Australia), aligned using the program BioEdit (Hall 1999) and refined by eye. PAUP* 4.0b10 (Swofford 2002) was used to compute the uncorrected pairwise distances for all sequences (tab. 3.1.3-4).

Tab. 3.1.3-1: Measures [mm] of West African *Astylosternus*. For abbreviations see app. 3.1.3-3.

Species / sex (N)		SVL	HW	FL	TF	TFT	LFF	LSF	ST
<i>A. occidentalis</i>	(♀; 45) mean±sd	55.9±3.4	19.8±1.7	24.5±2.1	26.1±1.9	36.6±3.1	8.8±1.1	6.9±0.7	4.3±0.5
	(♀; 45) min-max	47.5-65.3	16.3-24.6	18.7-29.5	20.7-30.1	29.5-42.9	6.4-11.8	5.4-8.1	3.4-5.5
	(♂; 34) mean±sd	52.0±4.5	18.6±2.1	22.6±2.0	24.6±2.4	34.3±3.3	8.3±1.1	6.5±0.9	4.5±1.0
	(♂; 34) min-max	44.5-61.8	15.1-22.4	19.3-27.2	19.3-29.0	27.7-40.5	6.2-11.7	4.9-8.7	3.4-7.1
<i>A. laticephalus</i> sp. nov.	(♀; 9) mean±sd	58.3±4.5	24.1±1.9	26.8±1.9	27.4±1.1	39.9±1.4	10.0±0.5	7.0±0.9	4.5±0.6
	(♀; 9) min-max	51.8-64.4	21.5-26.5	24.0-28.7	25.2-28.5	47.8-41.6	9.4-10.6	5.1-8.3	3.8-5.4
	(♂; 2) min-max	48.7-53.8	19.2-20.6	22.8-24.5	23.4-25.3	35.2-37.4	8.6-9.1	6.0-6.3	3.6-4.1
sp. Mont Péko	(♂; 2) min-max	51.8-66.5	20.0-24.4	20.2-29.0	24.2-27.3	35.0-43.9	7.5-9.4	5.9-7.2	4.1-5.0
		LIM	ED	IOD	IND	DEN	DNS	TD	
<i>A. occidentalis</i>	(♀; 45) mean±sd	2.6±0.4	6.8±0.7	6.7±1.2	4.7±0.4	5.0±0.5	4.1±0.6	4.3±0.5	
	(♀; 45) min-max	1.8-2.6	5.5-8.5	4.2-9.8	3.9-5.5	4.2-7.1	2.9-5.7	3.5-5.9	
	(♂; 34) mean±sd	2.5±0.4	6.5±0.6	6.2±1.2	4.6±0.5	4.9±0.5	3.8±0.6	4.0±0.4	
	(♂; 34) min-max	1.8-3.2	5.5-7.8	4.5-8.4	3.6-6.0	3.9-5.9	2.6-4.8	2.9-4.6	
<i>A. laticephalus</i> sp. nov.	(♀; 9) mean±sd	2.5±0.3	7.2±0.6	7.6±0.7	4.1±0.2	5.6±0.3	4.2±0.7	4.7±0.5	
	(♀; 9) min-max	2.1-2.8	6.3-7.9	6.7-8.5	3.7-4.5	5.3-6.1	2.7-4.9	4.2-5.3	
	(♂; 2) min-max	1.9-2.2	6.8-7.3	6.7-7.5	3.8-4.0	4.6-4.8	3.9-4.0	4.0-4.2	
sp. Mont Péko	(♂; 2) min-max	2.8-3.7	6.7-8.4	7.5-8.4	4.1-5.1	4.6-5.8	4.1-5.6	4.1-5.0	

Tab. 3.1.3-2: Indices of body measures of West African *Astylosternus* (compare tab. 3.1.3-1). For abbreviations see app. 3.1.3-3.

Species / sex (N)		SVL/HW	SVL/FL	SVL/TF	SVL/TFT	FL/TF	LFF/LSF	ST/LIM
<i>A. occidentalis</i>	(♀; 45) mean±sd	2.8±0.2	2.3±0.2	2.1±0.1	1.5±0.1	0.9±0.1	1.3±0.2	1.6±0.4
	(♀; 45) min-max	2.6-3.3	2.0-2.6	1.9-2.5	1.3-1.8	0.8-1.1	1.2-1.6	1.2-2.3
	(♂; 34) mean±sd	2.8±0.2	2.3±0.1	2.1±0.1	1.5±0.1	0.9±0.1	1.3±0.1	1.8±0.4
	(♂; 34) min-max	2.4-3.3	2.1-2.6	1.9-2.4	1.3-1.8	0.8-1.0	1.1-1.6	1.1-2.8
<i>A. laticephalus</i> sp. nov.	(♀; 9) mean±sd	2.4±0.1	2.2±0.2	2.1±0.1	1.5±0.1	1.0±0	1.5±0.2	1.8±0.2
	(♀; 9) min-max	2.3-2.6	1.9-2.5	2.0-2.4	1.3-1.6	0.9-1.0	1.1-2.0	1.6-2.1
	(♂; 2) min-max	2.4-2.8	2.0-2.4	1.9-2.3	1.3-1.5	1	1.4	1.9
sp. Mont Péko	(♂; 2) min-max	2.3-2.6	2.2-2.6	1.5-2.1	1.0-1.5	0.8-1.3	1.3-1.4	1.4-1.5

We performed neighbour-joining (NJ), maximum likelihood (ML) and Bayesian reconstructions. For ML and Bayesian analyses parameters of the model were estimated from the data set using Modeltest 3.7 (Posada & Crandall 1998) and MrModeltest 2.3 (Nylander 2002), respectively. For the ML tree we used the PhyML 3.0 computer cluster of the Montpellier bioinformatics



platform (<http://www.atgc-montpellier.fr/phyml/>; Guindon & Gascuel 2003). Bayesian analyses were performed with MrBayes, version 3.12 (Huelsenbeck & Ronquist 2001). The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003). For the Bayesian reconstruction clades with posterior probabilities (PP) $\geq 95\%$ were considered strongly (significantly) supported. Additionally, we used bootstrap analyses with 1000 (for ML) and 20000 (for NJ) pseudoreplicates to evaluate the relative branch support in the phylogenetic analysis. Four positions (501, 504, 506, 512) which could not be unambiguously aligned have been excluded from the analyses. GenBank accession numbers are summarised in tab. 3.1.3-3.

Tab. 3.1.3-3: GenBank accession numbers of species of the family Arthroleptidae investigated (compare fig. 3.1.3-2; app. 3.1.3-1); ¹= holotype of *Astylosternus laticephalus* sp. nov.; ²= paratype; FR= forest reserve; NP= National Park; n.a.= no data available.

Genus	Species	Country / region	Collection #	GenBank #
<i>Astylosternus</i>	<i>laticephalus</i>	Ghana / Atewa range	ZMB 75449 ¹	JQ582775
<i>Astylosternus</i>	<i>laticephalus</i>	Ghana / Afao FR	ZMB 75459 ²	JQ582774
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	tissue sample 09_095	JQ582778
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	tissue sample 09_137	JQ582779
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	tissue sample 09_142	JQ582780
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	tissue sample 09_201	JQ582781
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	tissue sample 09_223	JQ582782
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Nimba	ZMB 75362	JQ582773
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Boffa	ZMB 75495	JQ582793
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Boffa	ZMB 75492	JQ582791
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Boffa	ZMB 75489	JQ582792
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Boké	ZMB 75360	JQ582769
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75466	JQ582783
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75462	JQ582784
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75467	JQ582785
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75468	JQ582786
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75469	JQ582787
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75463	JQ582788
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Fouta Djalon	ZMB 75351	JQ582772
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Mt. Béro	ZMB 75461	JQ582790
<i>Astylosternus</i>	<i>occidentalis</i>	Guinea / Ziamara FR	ZMB 75464	JQ582789
<i>Astylosternus</i>	<i>occidentalis</i>	Liberia / Putu	ZMB 75470	JQ582794
<i>Astylosternus</i>	<i>occidentalis</i>	Liberia / Putu	ZMB 75479	JQ582795
<i>Astylosternus</i>	<i>occidentalis</i>	Liberia / Putu	ZMB 75473	JQ582796
<i>Astylosternus</i>	<i>occidentalis</i>	Liberia / Putu	ZMB 75475	JQ582797
<i>Astylosternus</i>	<i>occidentalis</i>	Ivory Coast / Taï NP	ZMB 75350	JQ582770
<i>Astylosternus</i>	<i>occidentalis</i>	Ivory Coast / Sangbé NP	ZMB 75353	JQ582776
<i>Astylosternus</i>	<i>occidentalis</i>	Ivory Coast / Sangbé NP	ZMB 75354	JQ582777
<i>Astylosternus</i>	<i>occidentalis</i>	Sierra Leone / Loma Mts.	ZMB 75375	JQ582771
<i>Astylosternus</i>	<i>batesi</i>	Cameroon / Lipondji	AMCC 117649 (UTA A-44482)	FJ151071
<i>Astylosternus</i>	<i>diadematus</i>	n.a.	n.a.	AY341723
<i>Astylosternus</i>	<i>schioetzi</i>	Cameroon / Edib	ZMFK 67733	AF124108
<i>Arthroleptis</i>	<i>crusculum</i>	Guinea / Nimba	ZMB 74039	JN408732
<i>Scotobleps</i>	<i>gabonicus</i>	n.a.	n.a.	AF215341
<i>Trichobatrachus</i>	<i>robustus</i>	Cameroon	ZFMK 66453	AY523773



Tab. 3.1.3-4: Mean uncorrected interspecific pairwise divergence (536bp of 16S rRNA) between various species of the family Arthroleptidae (see tab. 3.1.3-3 for specific data); provided are range (lower half of the cross table), mean and standard deviation, as well as sample size (in parentheses; all upper half of cross table); the intraspecific distance within *Astylosternus laticephalus* sp. nov. was 0% (N=2); within *A. occidentalis* the intraspecific pairwise distance ranged from 0.0-1.75% ($\bar{x} \pm \text{sd}$: 0.73 ± 0.45 , N=351); abbreviations follow order in first left column.

Species	<i>A. lat.</i>	<i>A. occ.</i>	<i>A. bat.</i>	<i>A. sch.</i>	<i>A. dia.</i>	<i>T. rob.</i>	<i>A. cru.</i>	<i>S. gab.</i>
<i>Astylosternus laticephalus</i>		3.20±0.1 6 (54)	10.95±0. 25 (2)	11.59±0. 01 (2)	11.92±0. 01 (2)	11.19±0. 37 (2)	17.64±0. 04 (2)	19.13±0. 39 (2)
<i>Astylosternus occidentalis</i>	2.91- 3.72		10.36±0. 32 (27)	11.54±0. 42 (27)	11.58±0. 43 (27)	11.06±0. 41 (27)	17.23±0. 24 (27)	19.61±0. 49 (27)
<i>Astylosternus batesi</i>	10.77- 11.12	9.89- 11.49		---(1)	---(1)	---(1)	---(1)	---(1)
<i>Astylosternus schiotzi</i>	11.58- 11.59	11.03- 13.37	2.97		---(1)	---(1)	---(1)	---(1)
<i>Astylosternus diadematus</i>	11.91- 11.92	11.08- 13.42	4.06	3.28		---(1)	---(1)	---(1)
<i>Trichobatrachus robustus</i>	10.93- 11.45	10.31- 12.14	8.6	9.04	9.56		---(1)	---(1)
<i>Arthroleptis cruscolum</i>	17.61- 17.66	16.86- 19.09	16.9	16.74	17.36	16.54		---(1)
<i>Scotobleps gabonicus</i>	18.85- 19.40	18.80- 21.27	19.19	20.5	20.66	18.92	20.18	

3.1.3.4 Results

Morphology and genetics of West African *Astylosternus* populations

Astylosternus from the western (western Ivory Coast, Guinea, Liberia, Sierra Leone) and eastern (eastern Ivory Coast, Ghana) parts of the Upper Guinea rainforest block differ in morphological and genetic characters. Males of the western population are smaller than the respective females (Mann-Whitney-U test, $Z = 4.0009$, $p < 0.0001$, $N_{\text{males}} = 34$, $N_{\text{females}} = 45$; tabs. 3.1.3-1, 2; fig. 3.1.3-1). Females do not differ in size among populations, but eastern females have much broader heads than western females (SVL/HW; $Z = 4.6709$, $p < 0.0001$, $N_{\text{eastern}} = 9$, $N_{\text{western}} = 45$) and western males (SVL/HW; $Z = 4.1796$, $p < 0.0001$, $N_{\text{eastern}} = 9$, $N_{\text{western}} = 34$). The head width of eastern males exceed the average head width of western males, but sample size was too small ($N = 2$) to test for differences. All adult male *Astylosternus* have distinct nuptial pads on the thumbs (figs. 3.1.3-4e to 4g, 3.1.3-10a, b) and paired subgular vocal sacs, the latter visible as slightly loose, granular skin close to the angle of the mouth (figs. 3.1.3-4c, d, 3.1.3-5a, 3.1.3-10c). The skin of the vocal sacs is black in the two males of the eastern population and can be black ($N = 16$) or white ($N = 12$) in males of the western population. Two males from Mont Péko (Ivory Coast) have dark grey vocal sac skin (fig. 3.1.3-4c). Almost all males of the western population (32 out of 34) and the two males from Mont Péko have very distinct spines along the ventral border of the lower mandible (figs. 3.1.3-3, 3.1.3-4c to 4d). These spines are arranged in 2–4 parallel rows and extend to the angle of the mouth. The two males of the eastern population, although in breeding condition, show no trace of such spines (fig. 3.1.3-10c). Almost all males of the western population (29 out of 34) and the two males from Mont Péko have very distinct spines on the belly (fig. 3.1.3-5). The two males of the eastern population again show no trace of such spines. In some western males, the spines on mandible and belly are hard to see (not black), but still clearly discernible (e.g. ZMB 75365; ZMB 75353; SMNS 9611). Frogs of the western and eastern populations further exhibit different colour pattern; the most remarkable difference being the presence of red dots on the back of eastern frogs and the lack of these dots, with a few exceptions, in western individuals (see below). Eastern frogs always have an iris which is reddish in its uppermost, dorsal, part. Western frogs exhibit a uniform greyish iris.

We compared approximately 536 bp of the 16S rRNA gene for 29 specimens from across eastern and western West African *Astylosternus* populations and three Central African

Astylosternus species (fig. 3.1.3-2, tab. 3.1.3-3). The mean uncorrected pairwise sequence divergence among West African *Astylosternus* populations, which form a monophyletic group, was 3.2% (range 2.9–3.7%). The three Central African *Astylosternus* species differed from each other by a mean of 3.4% (range 3.0–4.1%) uncorrected pairwise sequence divergence, thus exhibiting almost the same genetic divergences on the species level as observed in the two, western and eastern, West African clades (tab. 3.1.3-4).

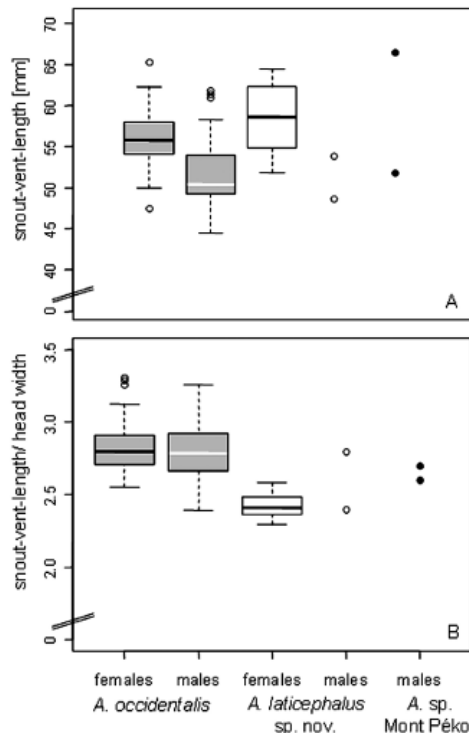


Fig. 3.1.3-1: Box plots of snout-vent length (A) and snout-vent length / head width (B) in adult West African *Astylosternus* taxa. Given are median and 25 and 75% quartiles. *Astylosternus laticephalus* sp. nov. females have broader heads than *A. occidentalis*. Sample sizes: *A. occidentalis*: females: 45, males: 34; *A. laticephalus* sp. nov. females: 9, males: 2; *A. sp.* Mont Péko males: 2 (compare text).

As *Astylosternus* populations from the western and eastern parts of the Upper Guinea rainforest zone clearly differ by morphological and genetic characters, we below re-describe the western *A. occidentalis* and describe the eastern populations as a new species. Frogs from Mont Péko National Park may possibly represent a third West African species. In particular their tadpoles were found in a rather unusual habitat. Unfortunately we had only two adult male frogs, preserved in formalin, available. As these two frogs, on the bases of morphology, were only weakly different to other western West African *Astylosternus* populations, we treat these two frogs separately, but within the *A. occidentalis* account.

The systematic position of *Astylosternus*

An unexpected outcome of our genetic comparison was that the genus *Astylosternus*, as so far defined, might be paraphyletic (fig. 3.1.3-2). Currently the family Arthroleptidae is believed to comprise about 144 species in eight genera (*Leptopelis*, *Arthroleptis*, *Cardioglossa*, *Scotobleps*, *Astylosternus*, *Trichobatrachus*, *Nyctibates*, *Leptodactylodon*; Frost *et al.* 2006; Pyron & Wiens 2011; Blackburn & Wake 2011). Frost *et al.* (2006) and Pyron & Wiens (2011) found *Trichobatrachus robustus* Boulenger, 1900 to be the sister taxon of *Astylosternus*; however, neither study included West African *Astylosternus*. Thus, our results agree with previous studies but the inclusion of taxa from throughout West Africa potentially provides a more rigorous test of *Astylosternus* monophyly. None of our analyses recovered strong support for the monophyly of *Astylosternus*. The West African

Astylosternus are the sister group to a clade comprising *Trichobatrachus* and the Central African *Astylosternus* (fig. 3.1.3-2) in our NJ tree. However, this grouping was insufficiently supported in ML and Bayesian Inference analyses. Thus, no conclusions can be drawn and this question remains to be tested with more extensive datasets. The mean uncorrected pairwise sequence divergence between the three Central and the two West African *Astylosternus* taxa ranged between 10.4–11.9%. This was even higher than the genetic similarity between Central African *Astylosternus* and *Trichobatrachus* (8.6–9.6% sequence divergence; tab. 3.1.3-4).

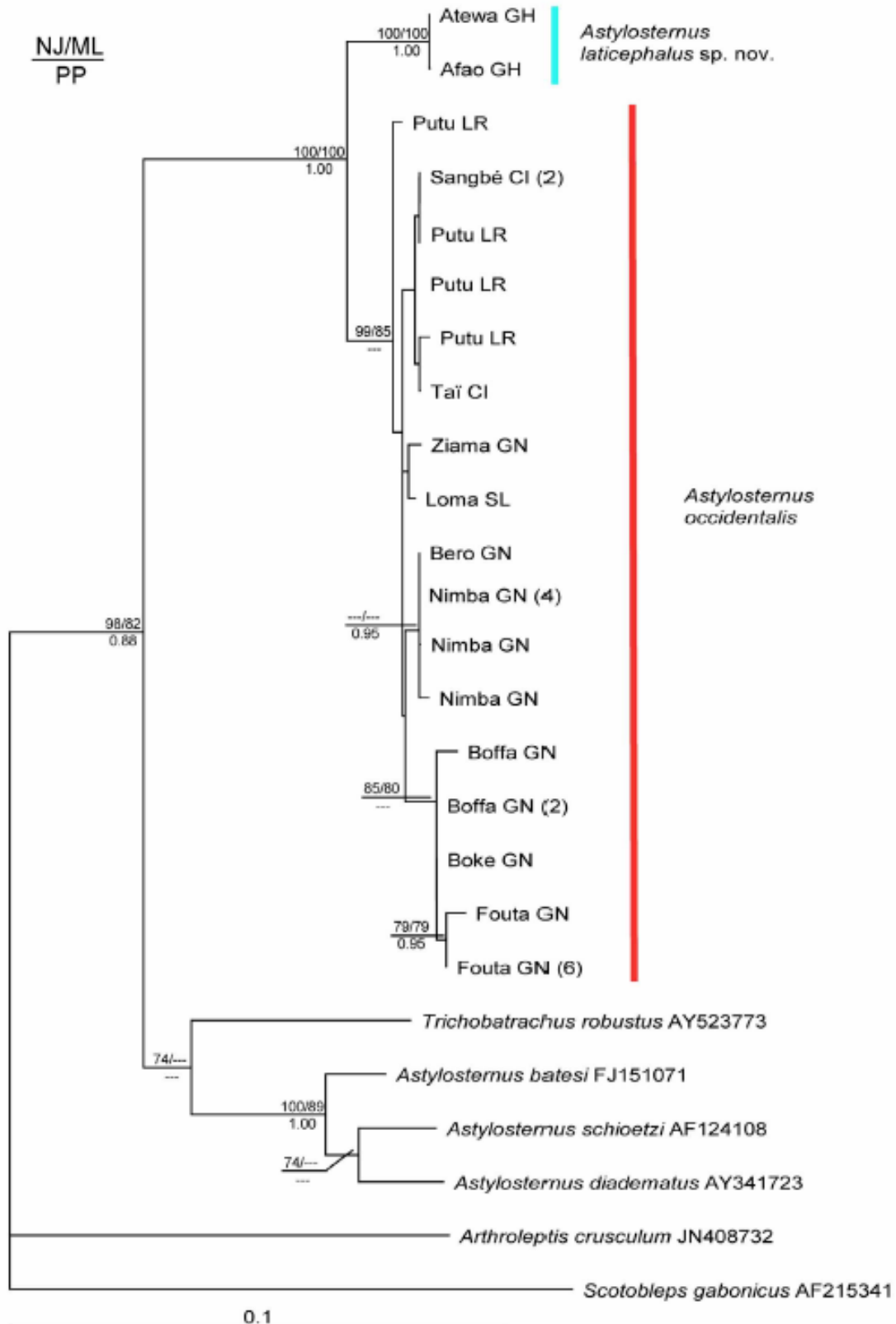


Fig. 3.1.3-2: Neighbour-joining consensus of the two West African *Astylosternus*, three Central African *Astylosternus* species, *Trichobatrachus*, *Scotobleps* and the type genus (*Arthroleptis*) of the family Arthroleptidae; based on a 536 bp fragment of the 16S rRNA gene. Included are single haplotypes per locality (numbers in brackets: specimens with respective haplotype). Given are bootstrap values (NJ, ML) and Bayesian posterior probability values (PP), sites and country (compare fig. 3.1.3-8, the type series, tab. 3.1.3- 3, and app. 3.1.3-1 for exact localities and GenBank accession numbers); CI= Ivory Coast; CM= Cameroon; GH= Ghana; GN= Guinea, LR= Liberia, SL= Sierra Leone.

Species accounts

Astylosternus occidentalis Parker, 1931 (figs. 3.1.3-3 to 7)

Astylosternus occidentalis Parker, 1931, Ann. Mag. Nat. Hist., Ser. 10, 7: 492. Holotype: BMNH 1947.2.5.48. Type locality: "Sandaru, E. Sierra Leone" collected on 24 June 1930 by G.L. Bates.

Hylambates yalense Angel, 1944, Bull. Mus. Natl. Hist. Nat., Ser. 2, 16: 420. Holotype: MNHNP 1944.128; female, 64 mm. Type locality: French Upper Guinea, Yala; in secondary forest, Mont Nimba region, Guinea. Synonymy with *Astylosternus diadematus* by Guibé, 1950 "1948", Cat. Types Amph. Mus. Natl. Hist. Nat.: 58. Synonymy with *Astylosternus occidentalis* by Lamotte, in Schiøtz, 1967, Spolia Zool. Mus. Haun., 25: 67.

Astylosternus diadematus sensu Lamotte & Zuber-Vogel 1954, Bull. Inst. fond. Afr. noire, Sér. A, 16, 1222.

Astylosternus occidentalis sensu Guibé & Lamotte 1958, Mém. Inst. fond. Afr. noire, 53, 261.

Material studied. See app. 3.1.3-1.



Fig. A3.3 - Dorsolateral, dorsal and ventral view of *Astylosternus occidentalis* holotype (BMNH 1947.2.5.48), an adult male from Sanduru, Sierra Leone. The inset pictures illustrate nuptial pads on left thumb and row of spines along lower mandible; spines on belly are visible on ventral view picture.

Re-description of the holotype [BMNH 1947.2.5.48; fig. 3.1.3-3; measures in mm]. The adult male has a snout-vent length of 59.3 (63 according to original description; Parker 1931); snout rounded in dorsal view, obtuse in lateral view, longer than eye diameter; head width 22.3, head as long as broad; interorbital distance (8) narrower than length of upper eyelid; large protruding eyes, diameter 7.6; pupil vertically elliptic; tympanum large, distinct and vertically elliptic, diameter 4.5, 2/3 of eye diameter; distance eye-nose only slightly larger (5.3), than distance nose-snout tip (4.8), internarial distance 4.7; canthus rostralis distinct and curved, slightly bulging; loreal region concave; vomerine teeth in two short transverse rows between choanae; supratympanal fold distinct, bending from posterior corner of eyelid ventrad to a position in-between angle of mouth and forearm base; hypertrophied forearm; first finger 8.8, longer than second, 6.3; relative finger length: $III > I > II \geq IV$; no digital webbing; femur length 23.7, shorter than tibia 28.2; foot with longest toe 36.8; finger and toe tips slightly broadened

without forming discs; sub-articular tubercles very prominent; relative toe length: $IV > III > V > II > I$; distinct rudiments of webbing on toe bases; no skin fringes along toes; inner metatarsal tubercle (3.0) almost as long as shortest toe; outer metatarsal tubercle absent; skin on back "smooth" (very small spines present everywhere, only visible with higher magnification), i.e. no warts or ridges; paired vocal sac mediad to angle of mouth; vocal sac skin granular and coarsely folded; spines on lower mandible, arranged in 2–3 rows parallel to lower lip; spines conical with dark tip; large nuptial pads on thumb; scattered small spines along lateral edges of other fingers and beneath tympanum; conical spines on belly (dark in original description; possibly faint); skin on outer part of thighs granular; skin on dorsal parts of body light brown, irregularly beset with small, roundish, dark brown spots; snout tip darker; light inter-ocular bar, posteriorly bordered by dark marking; iris uniform grey; lateral aspects of head beige, tympanum darker, upper lip with two dark bars; brown on flanks towards belly gradually fainting; limbs with indistinct brown transverse, partly interrupted bars; outer parts of thighs and sole of foot darker; ventral parts of skin yellowish white; vocal sac white like belly.

Additional characters not assessed in holotype and variation. Mandible with single, small, tooth-like process in front of lower jaw, with socket in between pre-maxillae; upper pre-maxillae and maxillae with numerous teeth; vomerine teeth in form of two hemispherical odontophores, perpendicular to body axis, not in contact to each other medially, each odontophore with row of teeth like tips; distance from odontophores to elliptical choanae ranging from slightly larger to slightly smaller than maximum length of odontophores; choanae smaller than odontophores; tongue broadly heart shaped, deeply notched anteriorly, densely beset with small papillae, extends along entire length of lower jaw; posterior 2/3 of tongue free.

Females are larger than males; otherwise measures and body ratios do not differ substantially between sexes (summarised in tabs. 3.1.3-1 and 2). Males have external vocal sacs, which can be white to deep black; dark brown to black nuptial pads (see below), slightly hypertrophied forearms and skin along canthus rostralis more prominent, slightly swollen; the latter region in females much less distinct. Breeding males from Guinea with black spines in pectoral region (fig. 3.1.3-5b; not seen in males from Ivory Coast, Liberia and Sierra Leone; spines exhibiting same colour as rest of belly, but see above for holotype); spiny ventral area slightly converging towards and almost reaching vent; caudal half of ventral surface of shanks with honeycomb-like structure, in each comb a black roundish spine; respective surfaces of females smooth or slightly granular (caudad part of shanks). Whereas spines on breast and belly in breeding males (black nuptial pads on thumb) of all populations are almost always present, spines on shanks may be absent (ZMB 75469, 75468, both males with black nuptial pads on thumb and black spines on throat) or only weakly developed. Spiny pectoral area with loose black skin on otherwise white venter in males from western Guinea (fig. 3.1.3-5a), skin loosens or even disappears in preservation; in these males the throat along the lower mandible is almost black and males from Boffa have distinct spines in the angle of the mouth (less distinct or absent in others). No or only traces of pedal webbing (fig. 3.1.3-4h).

The dorsal colour varies significantly between and within populations (fig. 3.1.3-6a to 6p) and ranges from almost uniform coloured dorsal surfaces in grey, beige, yellow, orange, light and dark brown; to animals with regular or irregular dark spots on back; spots or bars on extremities; unmarked flanks and flanks with darker spots. A clear intra-ocular band is almost always visible, as is a dark barred upper lip. The most common colour patterns are shown in fig. 3.1.3-6a, b and d, respectively. Rarely animals with a chocolate brown back and an irregular pattern of reddish spots have been found (e.g. two females: ZMB

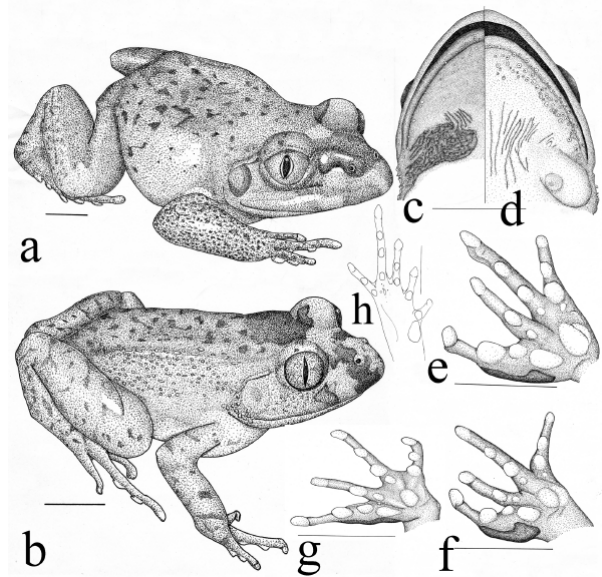


Fig. 3.1.3-4: Dorsolateral view (a, b), throat (c, d), left hand (e-g) and right foot (h) of adult male *Astylosternus* from the western part of the Upper Guinea forests: *Astylosternus* from Mont Péko (SMNS 9615: a, c, e, h; 66 mm SVL, the largest West African *Astylosternus* male so far known; SMNS 9616: f) and *A. occidentalis* from Tai National Park, Ivory Coast (b, d, g; scale bars = 1 cm).



Fig. 3.1.3-5: Ventral view of two adult *Astylosternus occidentalis* males in breeding condition, please notice spines on lower mandible, ventral parts of thighs, breast and belly, black skin layer on breast and nuptial pads on thumb, as well as whitish / greyish vocal sac skin; a) ZMB 75491, Boffa region, western Guinea; b) ZMB 75465, Ziamia forest, south-eastern Guinea.

75375 from Loma mountains; ZMB 75361 from the Western Area Peninsula Forest Reserve, fig. 3.1.3-6i, both Sierra Leone). On Simandou we found one frog with olive spots on the back, the edges of these spots beset with black points (fig. 3.1.3-6h). ZMB 75473 shows an especially pronounced dotted back pattern, being light beige with black spots where the edges of spots are darker than their interior part. In contrast, ZMB 75479 (fig. 3.1.3-6e) is more or less greyish, exhibiting a “dirty” pattern without distinct black spots or dots. Animals from Ivory Coast, i.e. the region of Taï National Park, most often were yellow with small black points (fig. 3.1.3-4b). Whereas some specimens have distinct black bars on fore and hind limbs (fig. 3.1.3-6a, k, n); others have uniform (fig. 3.1.3-6c, d, f) or a mottled limb pattern (fig. 3.1.3-6g). The iris colour of all specimens was uniform grey. Throat and belly white to flesh coloured (exception some breeding males, see above), throats may be also speckled with dark brown patches, in some individuals (e.g. ZMB 75479) belly almost translucent; lower side of extremities grey to fleshy pinkish. Overall males seem to exhibit more often darker colours with less distinct pattern than females. These colour patterns all faint in preservation, usually resulting in specimens with beige to dark brown backs, black points and dots usually remaining discernible.

The dorsal skin texture ranges from almost smooth (fig. 3.1.3-6e), to slightly granular (fig. 3.1.3-6g, i), irregularly beset with longish flat warts (fig. 3.1.3-6f), to animals which exhibit a more or less smooth back skin and flanks with discontinuous longitudinal rows of narrow ridges (fig. 3.1.3-6a). We could not detect a consistent pattern of skin texture correlated with sex, age or season (e.g. breeding versus non-breeding animals).

Advertisement call:

Described by Schiøtz (1964b) based on a specimen (ZMUC R 074932) from Kassewe, Sierra Leone. The call consists of two parts. The first part seems to be very similar to a call which we heard from *Astylosternus* from Mont Péko and which resembled the deep rattling call of some *Ptychadena* e.g. *Ptychadena* cf. *schillukorum* (Schiøtz 1964b as *Abrana floweri*; Rödel, unpubl. data). The second, buzzing note was often heard alone, the first note was always followed by the second. *Astylosternus occidentalis* from Taï National Park, Ivory Coast, uttered a buzzing call only.

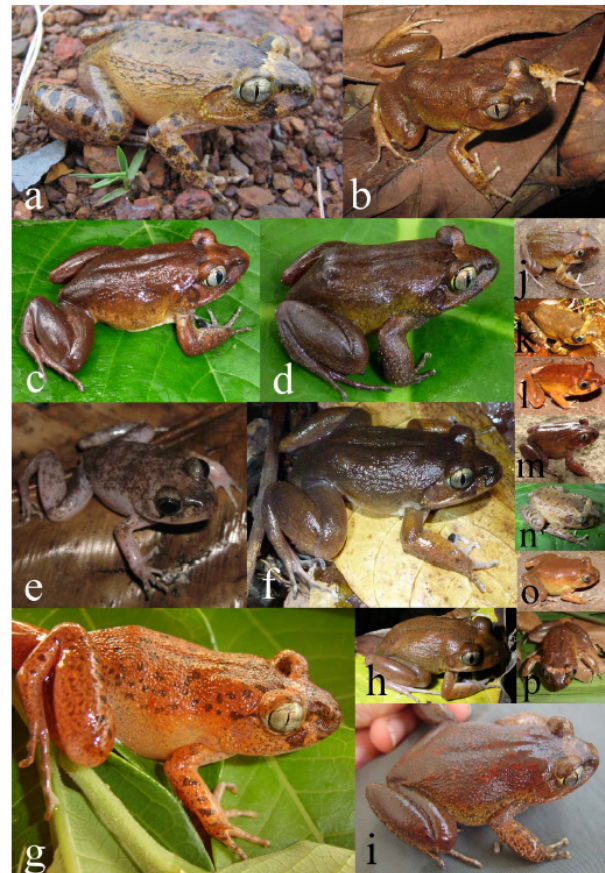


Fig. 3.1.3-6: Variation of life colouration in *Astylosternus occidentalis*, note differing back pattern and skin structure, as well as uniform grey coloured irises; a) female, Mount Nimba, south-eastern Guinea; b) ZMB 75475, female, Putu Range, eastern Liberia; c) and d) males, Boffa region, western Guinea; e) ZMB 75479, female, Putu Range; f) male, south-western Guinea; g) female, Mount Nimba; h) male, Simandou Range, south-eastern Guinea; i) ZMB 75361, female, 57.9 mm, Western Area Peninsula Forest Reserve, Sierra Leone; j) female, Fouta Djallon, Guinea; k) female, Mount Nimba; l) juvenile, Simandou Range; m) female, Fouta Djallon; n) ZMB 75475, male, Seliti, Sierra Leone; o) ZMB 75464, female, Ziama forest, south-eastern Guinea; p) female, Gola forest, western Liberia.

Tadpole [description based on Lamotte & Zuber-Vogeli 1954 and tadpoles stored in MNHN and ZMB, see app. 3.1.3-1]:

Extotrophic, lentic tadpoles; Gosner Stage 25–35 larvae with: body elongate almost rectangular in dorsal, slightly ovoid in lateral view (fig. 3.1.3-7a), sides of body almost parallel; large lateral sacs originating posterior to eye run along flanks, less distinct in smaller than in large larvae; snout in dorsal view broadly rounded, a bit more pointed in lateral view; small eyes, positioned dorsolaterally; nares small, positioned dorsolaterally, closer to snout tip than to eyes; oral apparatus in anteroventral position; dorsal lip wide and smooth, with large anterior gap between marginal papillae; lateral papillae in multiple rows; ventral lip with large, uni- or biserial marginal papillae; upper jaw sheath massif, broad U-shaped, with strongly serrated margin; lower jaw sheath massif, V-shaped, margin strongly serrated; Stage 25 tadpoles and older have a labial tooth-row formula of 1:2+2/2+2:1

or 1:1+1/2+2:1; all keratodont rows on skin sheaths; keratodonts set very dense to each other; labial keratodonts unidenticulate, connected by hyaline skin reaching almost tips of keratodonts; vent tube dextral; spiracle sinistral; very long tail axis (approx. 2.5 times body length); tail axis height exceeds height of dorsal and most parts of ventral fin; dorsal fin originates slightly posterior to tail body junction; dorsal fin almost parallel to tail axis up to tail tip; ventral fin mostly narrower than tail axis, only in last third broader than tail axis; ventral fin almost parallel to tail axis; tail tip rounded; lines of pores (probably neuromast canals making up a side line system) starting on snout-tip; extending dorsally between eyes in two parallel rows to insertion of dorsal tail fin, below eyes dorsal from spiracle to about mid-body on flanks; pore rows circumventing eyes; visibility of pore rows better in younger stages; body more or less uniform dark brown to almost black, tail fin dark brown to almost black in last third of tail.

The largest tadpole, Gosner Stage 37, measured 29.2/94.3 (body length/total length). Metamorphosing froglets (with rests of tail) measured 27.5–35.7 mm SVL ($x \pm \text{sd}$: 32.3 ± 2.8 ; $N = 10$). Parker (1936) reported tadpoles collected in Liberia, the largest larvae with fully grown hind limbs measuring 88 mm (61 mm to the tail); a freshly metamorphosed froglet had a SVL of 30 mm. Lamotte & Zuber-Vogeli (1954) hint on the delayed appearance of the extremities, an adaptation to maintain, as long as possible, a good swimming performance in fast flowing habitats. Guibé & Lamotte (1958) mention tadpole sizes of close to 10 cm shortly before metamorphosis. Parker (1936) hints on the similarity of his tadpoles (body shape, proportions and dentition) with Angel's (1930) description of *Gampsosteonyx batesi* (tadpoles from Fouban, Cameroon; thus most likely being tadpoles of *A. diadematus*).

Natural history:

Astylosternus occidentalis occurs along swift to fast-flowing creeks and streams in dense forest from almost sea level (130 m) to about 1300 m a.s.l. (Guibé & Lamotte 1958; Böhme 1994; this study). Its habitats may consist of primary as well as degraded or fragmented forests within the rainforest zone or dense gallery forest in the southern part of the humid Guinea savannah zone (Rödel & Branch 2002; Ernst & Rödel 2006; Ernst *et al.* 2006; Hillers & Rödel 2007; Hillers *et al.* 2008b; this study). The species is usually not abundant and patchily distributed, similar to other anuran species associated with rivers in forests of hilly or mountainous areas (Lamotte 1966). In Mont Sangbé National Park individuals were observed within the forest in a steep valley (Rödel 2003). Whereas the vegetation on the valley ground and slopes consisted of rainforest trees, the hill tops carried savannah vegetation. One *A. occidentalis* male was found still within forest but only a few meters from true Guinea tree-savannah (Rödel 2003). Similarly *A. occidentalis*

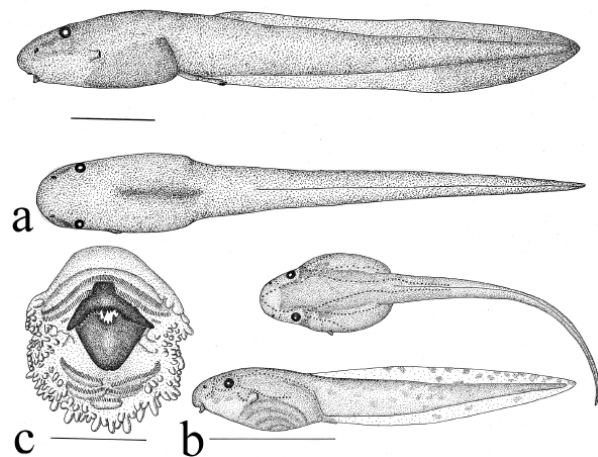


Fig. 3.1.3-7: Lateral and dorsal view and mouth part of typical *Astylosternus occidentalis* from Mount Nimba (a; Gosner stage 34) and *Astylosternus* tadpoles from Mont Péko (b, c; Gosner stage 25) tadpoles (scale bars in a & b: 1 cm; c: 1 mm).

has been recorded in gallery forest in the savannah zone of south-eastern and western Guinea (this study). Guinean specimens in particular have been regularly encountered in some distance to water. Most populations, however, were recorded within forest close to flowing water. Males are calling from the forest floor close to but not in water (Schjötz 1964b). In contrast to Central African *Astylosternus*, we never observed West African frogs of the genus using the terminal phalanges of their hind feet in defence (see Blackburn *et al.* 2008). However, phalanges of western and central African *Astylosternus* species are anatomically indistinguishable (Barej *et al.* 2010).

The reproduction behaviour is unknown. Tadpoles can usually be observed at night on the ground of slow or almost stagnant parts of forest creeks and rivers. Larger rivers as well as very small tributaries are inhabited. When disturbed tadpoles flee immediately into deeper and fast flowing water or burrow themselves into loose sediment of the shallow parts. Other anuran species which often occur in syntopy with *A. occidentalis* are *Amietophrynus togoensis* (Ahl, 1924), *Cardioglossa occidentalis* Blackburn, Kosuch, Schmitz, Burger, Wagner, Gonwouo, Hillers, & Rödel, 2008, *Leptopelis macrotis* Schjötz, 1967, *Phrynobatrachus liberiensis* Barbour & Loveridge, 1927, *Petropedetes natator* Boulenger, 1905, *Conraua* spp., and *Hyperolius chlorosteus* (Boulenger, 1915).

On Mont Péko, Ivory Coast (fig. 3.1.3-8) the local *Astylosternus*, in particular their larvae, behaved differently. We collected two males and tadpoles (see taxonomic remarks) close to the summit at about 1000 m a.s.l. at the border of a heavily overgrown shallow creek (Rödel & Ernst 2003), flowing over massive granite underground. These males were calling at night, well concealed in small cavities under stones close to the creek's bank. Several more males were heard but could not be exactly localised. The tadpoles were caught in shallow, slow flowing parts of the same creek and in very shallow (< 1 cm water height) flooded parts in the open moorlands (see fig. 2 in Rödel & Ernst 2003). Other frogs observed close to this site were *Ptychadena* cf. *schillukorum* (Werner, 1908) and *Hyperolius lamottei* Laurent, 1958 (Rödel & Ernst 2003).

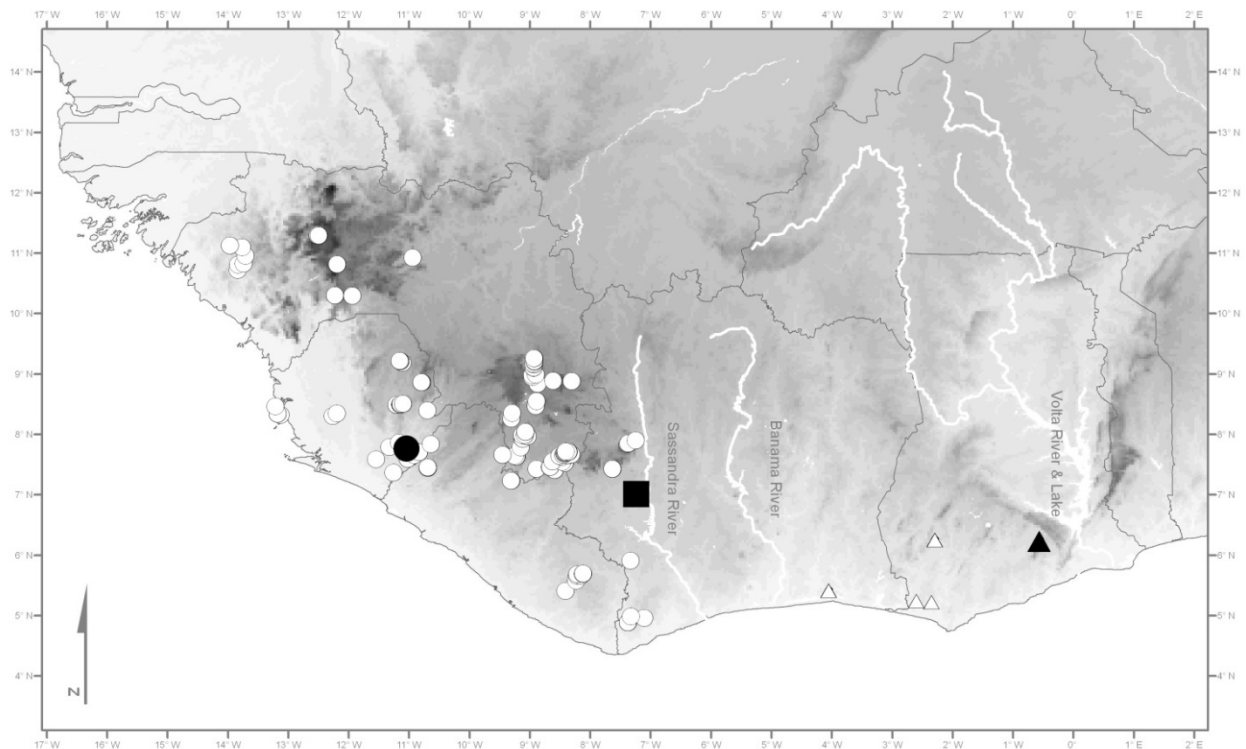


Fig. 3.1.3-8: Known records of West African *Astylosternus* taxa; circles: *Astylosternus occidentalis*, black circle: “type locality” (compare text); triangles: *A. laticephalus* sp. nov., black triangle: type locality; black square: Mont Péko, locality of *A. sp.* (for exact localities see app. 3.1.3-1); country boundaries, topography and three major rivers (Sassandra, Bandama, Volta) are indicated; map based on the ASTER Global Digital Elevation Model: www.ersdac.or.jp.

Astylosternus occidentalis is restricted to the western part of the Upper Guinean forests (fig. 3.1.3-8). Records have been published from Sierra Leone (Parker 1931; Schiøtz 1964a); Liberia (Parker 1936; Hillers & Rödel 2007); Guinea (Guibé & Lamotte 1958; Böhme 1994; Rödel & Bangoura 2004; Rödel *et al.* 2004; Hillers *et al.* 2006, 2008a); Ivory Coast (Rödel & Branch 2002; Rödel 2003; Ernst & Rödel 2006; Ernst *et al.* 2006; Hillers *et al.* 2008b). The type specimen was collected at Sandaru in Sierra Leone. We tried to localise this locality and identified two places with this name at 7.8 / -11.0 and 8.4 / -10.7, respectively. In the map (fig. 3.1.3-8) we have used the first coordinates to plot the “type locality”, although, we failed to identify any objective criteria on which we could decide whether the one or the other Sandaru was meant by Parker (1931). Both localities, however, are comparatively close to each other and well within the range of *A. occidentalis*. Records from Ghana (Hughes 1988) most likely are based on misidentifications of the species which is described below.

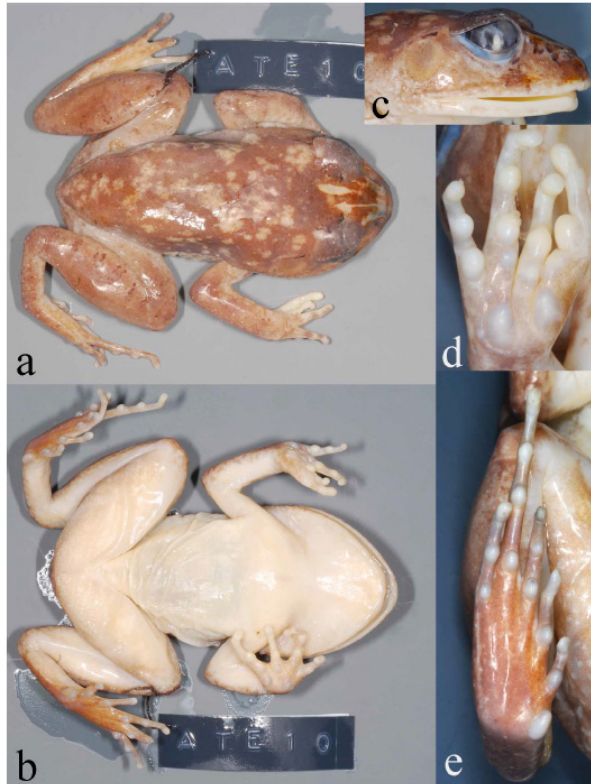


Fig. 3.1.3-9: *Astylosternus laticephalus* sp. nov. female (holotype, ZMB 75449, 58.6 mm) from Atewa Forest Reserve, Ghana; dorsal (a) and ventral (b) view, portrait (c); ventral views of right hand (d) and right foot (e).

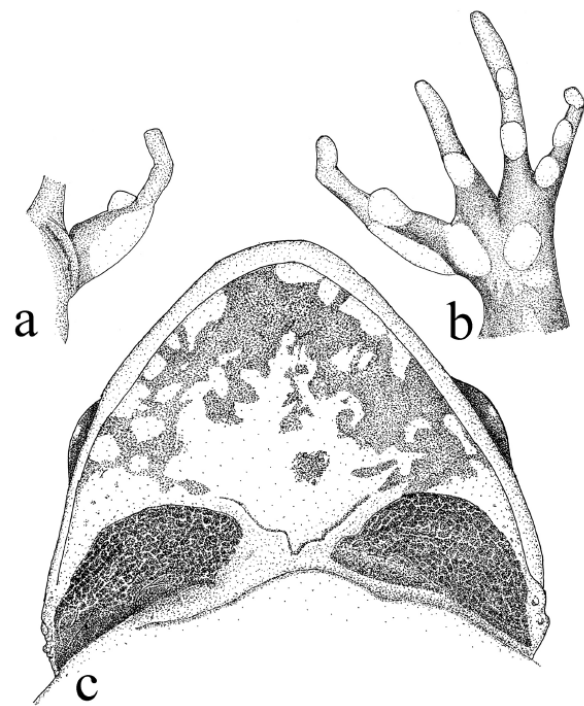


Fig. 3.1.3-10: Left thumb in dorsal view with nuptial pad (a), left hand in ventral view (b) and throat (c) of adult male *Astylosternus laticephalus* sp. nov. (paratype, MNHN 1999.7334, 48.7 mm) from Banco National Park, Ivory Coast.

Taxonomic remarks:

Hylambates yalense has been described from Mount Nimba, Guinea (Angel 1944; not 1940 as cited in Frost 2010). According to Ohler (pers. comm. February 2005) the type of *H. yalense* had been donated to the collection of the Institut Fondamental d'Afrique Noire in Dakar, Senegal. However, there it could not be traced (Seck, pers. comm. May 2005). According to the original description (Angel 1944) the type, a female of 64 mm SVL, would deviate from the *A. occidentalis* description given above by the following characters: nares in equal distance to eye and snout tip (instead of nares closer to snout); internarial distance equal to interorbital distance (instead of interorbital distance larger). All other characters listed by Angel (1944) are within the range of *A. occidentalis*. As the two differences might be simply due to different ways in taking these measures and as we had a large number of *A. occidentalis* vouchers and tissue samples available from Mount Nimba and surroundings (see app. 3.1.3-1), all of which were identical to other *A. occidentalis* populations, we follow Lamotte (in Schiøtz 1967) in regarding *Hylambates yalense* as a junior synonym of *A. occidentalis*.

The *Astylosternus* from Mont Péko National Park, Ivory Coast (figs. 3.1.3-4a, c, d; SMNS 9615, male, 66.5 mm; 67.6 mm in life, SMNS 9616, male, 51.8 mm; 55.6 mm in life, 7.0 / -7.2, 1 September 2000, densely overgrown creek on granite mountain, > 1000 m a.s.l.; coll. R. Ernst & M.-O. Rödel) appeared to differ from other *A. occidentalis* populations (compare Rödel & Ernst 2003). Their head width is in the range of the new species described below (tab. 3.1.3-2), thus wider than in typical *A. occidentalis*. One male (SMNS 9615) was larger than any other



Fig. 3.1.3-11: Life colouration of female and juvenile (c) *Astylosternus laticephalus* sp. nov. from Ghana, Ankasa Conservation Area (a, b, d, e, f, g) and Afao Hills Forest Reserve (c); b, d, f: MVZ 244910; c: ZMB 75459.

altered forest habitats, the current IUCN RedList classification of “Least Concern” should be kept. If new findings would proof the Mont Péko frogs being a separate species; this taxon would be highly threatened due to a restricted range of occurrence and very intense pressure of logging and other anthropogenic activities.

Astylosternus from the western Upper Guinea forests (fig. 3.1.3-1). They seemed to be more massive and had a smooth back skin (in life *A. occidentalis* granular skin, warts or ridges are usually discernible). For measures of both males see tabs. 3.1.3-1 and 2. At the same locality we collected tadpoles (ZMB 77194, fig. 3.1.3-7b, c; same collection details as SMNS 9615 and 9616). The larval habitat was different to that of other known *Astylosternus* populations (see above). A species endemic to the Mont Péko region in Ivory Coast would be in line with recent findings in other frog genera of similar ecological requirements (*Conraua* and *Petropedetes*; M.F. Barej & M.-O. Rödel unpubl. data). However, given the range of variation within the various *A. occidentalis* populations, further vouchers and genetic samples are needed to clarify the taxonomic status of the Mont Péko frogs.

Conservation status:

Given the rather wide distribution of the species, including various protected areas (i.e. Taï National Park, Sapo National Park, Mount Nimba Biosphere Reserve) and its apparent potential to survive in

Astylosternus laticephalus sp. nov. Rödel, Hillers, Leaché, Kouamé, Ofori-Boateng, Diaz & Sandberger (figs. 3.1.3-9 to 12)

Holotype. ZMB 75449 (field and tissue #: ATE10, female, 58.6 mm), Ghana, Atewa Forest Reserve, 6.23375 / -0.56557, 14 April 2007, forest around stream next to road, coll. C. Ofori-Boateng, A. Hillers & G. Segniagbeto.

Paratypes. Ivory Coast: MTD 48026 (field and tissue #: Ba04.24, female, 62.2 mm), ZMB 75454-75458 (Ba04.26, subadult, 45.5 mm; Ba04.25, female, 62.5 mm; Ba04.21, female, 64.4 mm; Ba04.22, subadult, 43.3 mm; Ba04.23, female, 58.4 mm;), Banco National Park, 5.41667 / -



4.10500, rainy season 2004, swampy forest, coll. N.E. Assemian, B. Tohé & G. Kouamé; MNHN 1993.6073 (male, 53.8 mm), 1999.7333 (female, 54.8 mm), 1999.7334 (male, 48.7 mm), 1999.7335 (female, 59.8 mm), 1999.7736 (female, 52.6 mm), 1999.7337 (female, 51.8 mm), Banco National Park, Abidjan; Ghana: ZMB 75459 (AF4, juvenile, 25.6 mm), ZMB 75459-75460 (AF3 juvenile; 26.7 mm; AF2, tadpole), Afao Hills Forest Reserve, 6.25461 / -2.29492, riparian forest around small stream in valley, coll. C. Ofori-Boateng & A. Hillers; ZMB 75450-75453 (COB90, juvenile, 34.7 mm; COB318, subadult, 40.8 mm; COB119, juvenile, 38.6 mm; COB123, juvenile, 31.7 mm), Western Province, Ankasa Conservation Area, pristine forest along streams in dry season, coll. C. Ofori-Boateng; MVZ 244910 (female, 67 mm), Ankasa Conservation Area, 5.28173 / -2.64022, 26 June 2004, wet evergreen forest area, trail adjacent to the bamboo cathedral, coll. A.D. Leaché & R. Diaz; MVZ 244909 (juvenile, 35 mm), 28 June 2004, approximately 1 km farther from the bamboo cathedral, other data as MVZ 244909.

Additional material:

ZMB 77461 (field# AF 03), tadpole, Ghana, Afao Hills Forest Reserve, 6.25461 / -2.29492, riparian forest around small stream in valley, coll. C. Ofori-Boateng & A. Hillers; ATE7 (tissue only), juvenile, 25.8 mm; ATE8 (tissue only), juvenile, 28.6 mm; ATE27 (tissue only), male, 45.6 mm, Ghana, Atewa Forest Reserve, 6.23375 / -0.56557, 15 April 2007, swampy area next to small stream, in valley in forest, coll. C. Ofori-Boateng, A. Hillers & G. Segniagbeto; COB2202 (collection Ofori-Boateng, Kumasi, Ghana), Ghana, Atewa Forest Reserve, coll. C. Ofori-Boateng; three adult specimens without number (amphibian reference collection at University Abobo-Adjamé, Ivory Coast), male (51.0 mm), females (60.0, 67.0 mm), Ivory Coast, Banco National Park, 5.41667 / -4.10500, 5 May 2004, forest close to Banco River, coll. N.E. Assemian, N.G. Kouamé & B. Tohé.

Diagnosis:

Astylosternus laticephalus sp. nov. has the typical body shape of frogs of the genus *Astylosternus*, however, with exceptionally broad heads, i.e. broader than in *A. occidentalis*; males of the new species without spines on throat and belly (always present in *A. occidentalis* males); males without nuptial black skin layer in pectoral region (present in male *A. occidentalis* from western Guinea); back brownish to brownish red, always with distinct red dots (red dots only rarely present in *A. occidentalis*); bicoloured iris, grey with a reddish upper third (*A. occidentalis* always with uniform grey iris). *A. laticephalus* sp. nov. differs from *A. occidentalis* by a mean of 3.2% (range 2.9-3.7%) in the investigated part of the 16S rRNA gene. Genetic divergence to the morphologically most similar Central African species, *A. diadematus*, was 11.9%.

Description of the holotype [measures in mm]:

The holotype is an adult female with a snout-vent length of 58.6; head width 22.7; head as long as broad; interorbital distance narrower than length of upper eyelid; snout rounded in dorsal view, obtuse in lateral view, longer than eye diameter; eyes large (7.9) and protuberant directed anterolaterally; interorbital distance 7.2; pupil vertically elliptical; eye diameter larger than tympanum diameter, 5.3; tympanum vertically elliptical; supratympanal fold from posterior vertical midpoint of orbit to meet with dorsal border of tympanic annulus, where descent is sharp and terminates at half the vertical diameter of the tympanic annulus dorsally to the axilla; nares closer to snout-tip (2.7) than to eye (5.5), nostrils oriented posterolaterally; internarial distance 4.4; canthus rostralis rounded and straight; loreal region slightly concave and gradually sloping laterally; single, small, tooth-like process at lower jaw symphysis, with corresponding socket in between premaxillae; upper premaxillae and maxillae with numerous teeth; vomerine teeth in form of two hemispherical odontophores, perpendicular to body axis, almost being in contact to each other medially, each with row of teeth like tips (5 left, 6 right); distance from odontophores to elliptical choanae slightly larger than maximum length of odontophores; choanae almost equal in size to odontophores; tongue broadly heart shaped, deeply notched anteriorly, densely beset with small papillae, extends over entire length of lower jaw; posterior 2/3 of tongue free.

Forelimbs robust, fingers slender and long; prepollex absent; first finger 10.3, almost double the length of second finger (5.1); relative finger lengths I>III>II>IV; finger tips broadened without



forming discs; subarticular tubercles large, subconical, protruding distally; thenar and palmar tubercles large and elliptical; supernumerary tubercles absent; number of subarticular tubercles on digits I-IV: 1, 1, 2, 2; no digital webbing; hind limbs short and robust; femur length 28.3, almost equal to tibia 28.4; tibia-fibula with longest toe 38.4; relative toe lengths IV>III>V>II>I; shortest toe (4.2) almost double the length of inner metatarsal tubercle (2.3); inner metatarsal tubercle large, elliptical; toe tips broadened without forming discs; number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent; traces of webbing between toe bases; no skin fringes along toes. Tip of toe IV on left foot missing.

Skin on head, back, belly and throat predominantly smooth; small whitish spines scattered on back, dorsal parts of extremities and eyelids; white warts posterior to angle of mouth, ventral from tympanum; posterior region of thighs areolate; irregularly spread narrow low tubercles along flanks; no tubercles or warts on forearms or interocular region; head with white scratches (scars).

Base colour of dorsum in preservation is a light brown to reddish brown; back with irregularly arranged and shaped light beige spots; upper eyelids greyish; head laterally with two darker bars, the posterior one below eye; upper and lower lips white; supratympanic fold anteriorly rimmed thin black; warts on flanks beige; forelimbs dorsally light brown, slightly mottled beige, first two fingers almost uniform white; hind limb colour as forelimbs, dark bordered cross bars indicated in thighs (4) and lower legs (5-6); throat, belly, ventral parts of fore- and hind limbs uniform white or creamish; only ventral part of feet reddish brown, metatarsal tubercle and subarticular tubercles creamish white.

Variation:

Females seem to be larger (up to 67.0 mm; MVZ 244910) than males (53.8 mm), although the small sample size of the latter (N= 2) does not allow for generalization. The tympanum shape varies between vertically elliptical (most vouchers) to round; the supratympanic fold is sometimes thin to absent; sometimes tympanic membrane prominent within faint tympanic annulus. Other measures and indices identical between the two sexes; values are summarized in tabs. 3.1.3-1 and 3.1.3-2.

Dorsal and lateral skin texture can consist of many irregularly spaced small roundish warts, not arranged in rows, sometimes fused to small ridge like structures (fig. 3.1.3-11). Males have paired subgular vocal sacs, visible in preserved frogs as slightly loose, granular black skin near the angles of the mouth; males with large brown nuptial pads on the external side of the thumb. Canthus rostralis in males more prominent bulging and rounded; males with more massive forearms than females. In contrast to other western West African *Astylosternus*, *A. laticephalus* sp. nov. males in breeding condition, lack spines on throat and belly.

The dorsal base colouration in life consists of a light grey, brown, reddish brown or almost black; all specimens exhibit a more or less dense pattern of smaller to larger, irregularly shaped red spots on back; smaller black or brown spots may be present, in particular in juveniles; iris greyish, upper third reddish to orange; the anterior part of the eyelids bright yellow to red blotches, connected by a very conspicuous interorbital stripe of the same colour; snout tip and area posterior to interorbital stripe, including posterior part of eyelid, darker than rest of back, this pattern sometimes consisting of a symmetrical pair of triangular shaped black spots (fig. 3.1.3-11); frenal area dark as snout tip; loreal area distinctly lighter coloured than snout tip; light infraorbital band; supratympanic ridge usually bordered by thin black line; fore and hind limbs with or without distinct black cross bars; lateral colour gradually fading from back colour to whitish venter, with irregularly scattered black points; ventral colouration (throat and abdomen) creamish-white; ventral surface of thighs and arms creamish-yellow with reddish brown mottling around lateral margins of limbs.

In preservative all patterns and colouration almost as in life, but faded; the red dorsal spots remain as light beige spots.

Tadpole [measures in mm; description based on ZMB 75460]:

Exotrophic, lentic tadpole; Gosner stage 39; total length 62.1; body broad almost as long as wide, slightly elliptical in dorsal, slightly depressed in lateral view (possibly a preservation artefact); body length 23.8; body width 24.2; sides of body slightly concave, snout in dorsal view broadly rounded, a bit more pointed in lateral view; large lateral sacs originating posterior to eyes run along flanks; small eyes, positioned dorsolaterally, pupil round; nares small, positioned dorsolaterally, closer to snout tip than to eyes; oral apparatus in anteroventral position; dorsal lip wide and smooth, with large anterior gap between marginal papillae; lateral papillae ventral lip with large, uni- or biserial marginal papillae; upper jaw sheath massif, broad U-shaped, strongly serrated margin, most central “tooth” most prominent; lower jaw sheath massif, V-shaped, margin strongly serrated; labial tooth-row formula 1:1+1/3; all keratodont rows on skin sheaths; labial keratodonts unidenticulate, connected by a hyaline skin; vent tube dextral; spiracle sinistral (almost invisible); very long tail axis (> 2.5 times body length); tail axis height largely exceeding height of dorsal and ventral fin, both fins very narrow; dorsal fin originates slightly posterior to tail body junction; dorsal fin almost parallel to tail axis up to rounded tip; no pores (neuromast canals) visible (possibly due to poor preservation or advanced developmental stage); body more or less beige, mottled with dark brown, tail fin brown to almost black in last third of tail. Newly metamorphosed froglets measured 25.6–28.7 mm (N= 2).

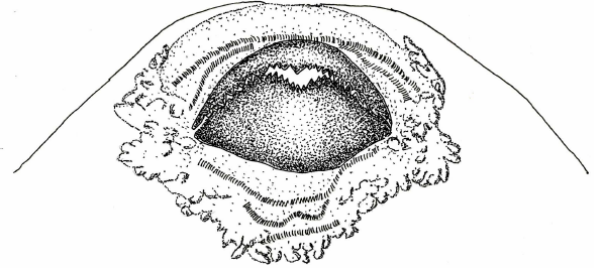


Fig. 3.1.3-12: Mouth part of a *Astylosternus laticephalus* sp. nov. tadpole from Afao Hills, Ghana (ZMB 75460; Gosner stage 39; SVL: 23.8 mm).

Natural history:

Not much is known about the biology of the new species. *Astylosternus laticephalus* sp. nov. lives in lowland rainforest habitats (fig. 3.1.3-13), mostly close to small or mid-sized streams (Rödel *et al.* 2005; Assemian *et al.* 2006). In Banco National Park, Ivory Coast we recorded the new species in the leaf litter of swampy areas in closed canopy forest, open forest and in natural forest gaps, both in close vicinity to the River Banco and in larger distance (about 1 km) from the river (Assemian *et al.* 2006). A total of 12 specimens were only observed during the rainy season, 11 of them during the night. In the Ankasa Conservation Area we found the new species in wet evergreen forest on a trail adjacent to the Bamboo Cathedral (fig. 3.1.3-13).



Fig. 3.1.3-13: Rainforest habitats of *Astylosternus laticephalus* sp. nov.; streams in Ankasa Conservation Area (a, b), and forest in Atewa Forest Reserve (c) and Ankasa Conservation Area (d), Ghana.

Distribution:

So far *A. laticephalus* sp. nov. is known from one forest in eastern Ivory Coast, the Banco National Park (Assemian *et al.* 2006), and various sites in Ghana: Afao Hills Forest Reserve, Draw River Forest Reserve and Ankasa Conservation Area in south-western Ghana (Rödel *et al.* 2005; this paper), and Atewa Range in southern-central Ghana (fig. 3.1.3-8). The latter site was chosen as type locality of the new taxon to underline the outstanding importance of this mountainous region for the Ghanaian biodiversity.

Conservation status:

The distribution of the species from eastern Ivory Coast to southern-central Ghana, including various protected areas (i.e. Banco National Park, Afao Hills Forest Reserve, Ankasa



Conservation Area), seems to imply a IUCN Red List classification of “Least Concern”. However, rainforests in south-eastern Ivory Coast are under intense logging pressure and highly fragmented. Forests in south-western Ghana are better protected but likewise fragmented and the Atewa Range is currently under threat because of small scale mining activities and further plans to mine for gold, diamonds and bauxite on an industrial scale. We thus suggest classifying the new species as “Near Threatened”.

Etymology:

The name derives from the Latin words *latus* for wide and the Greek *Κεφάλι* for head, referring to the conspicuous wide head of the new species.

3.1.3.5 Discussion

Due to large intra-specific variation, species within the genus *Astylosternus* are difficult to characterize morphologically (Amiet 1977). However, *A. laticephalus* sp. nov. differs distinctly from *A. occidentalis* in various morphological characters, i.e. a broader head, a back pattern with red dots (rarely present in *A. occidentalis*), a bicoloured iris and the lack of spines on the throat, pectoral region and belly in males. These morphological differences are supported by the genetic difference in the investigated part of the 16S rRNA gene. Thus the new species could be unambiguously characterized. It seems that the uniqueness of *Astylosternus* from eastern Ivory Coast has already been recognized by Amiet (1977) who mentions, in a foot note, an *Astylosternus* from Ivory Coast, collected by J.-L. Perret. According to J.-L. Amiet this frog was most similar to his diadematus-group (comprising *A. diadematus*, *A. batesi*, *A. montanus* Amiet, 1978”1977”) of Central African *Astylosternus* species.

With respect to these three Central African species the two West African species, superficially, are most similar to *A. diadematus*. The latter, distributed in lower and mid-altitude forests from eastern Nigeria to the Sanga River, exhibits a very characteristic pattern on the outer part of the shanks, consisting of sharply bordered yellow patches (white in preservation) on dark brown ground (see fig. 26 in Amiet 1977; pattern still partly visible in the type – ZMB 13920 – although specimen in bad condition). This pattern is not present in neither *A. occidentalis* nor *A. laticephalus* sp. nov. *Astylosternus diadematus* is also slightly smaller than the West African species (mean SVL in 35 males: 47.8 mm; Amiet 1977). Concerning body size the two West African species are within the range of the larger species of the genus (Amiet 1977).

In his monographic revision Amiet (1977) defined further *Astylosternus* species groups. Amiet’s (1977) perreti-group is characterized, among other features, by the nuptial pads on male thumbs, consisting of two parts. All other Central as well as the West African species have one large nuptial pad on the thumb. Concerning the colour pattern the West African species, in particular *A. occidentalis*, are somehow intermediate between Amiet’s (1977) perreti- and the schioetzi/diadematus/nganhanus-groups. Concerning the ventral colouration, West African species are more similar to the rheophilus-group, having a white belly instead of a yellow one as in most Central African *Astylosternus*. The belly skin of Central African male *Astylosternus* is, with the exception of male *A. ranoides* Amiet, 1978”1977”, smooth. *A. ranoides* possesses, as *A. occidentalis*, spines in the pectoral region (Amiet 1977, 1989). Concerning the dorsal skin structure the West African taxa lack the very conspicuous ridges of the perreti-group, but exhibit more structure than the almost smooth *A. rheophilus* Amiet, 1978”1977” and *A. nganhanus* Amiet, 1978”1977” and are thus again most similar to the diadematus-group. However, the skin structure differs not only between, but partly also within species (Amiet 1977; this study). According to Amiet (1977) these structures may vary, in particular with respect to the physiological and environmental conditions of a frog. In summary, the West African *Astylosternus*, although most similar to the diadematus-group, are not clearly assignable to one of Amiet’s (1977) species groups. This is also underlined by our genetic data which show that West African *Astylosternus* form one clade which is not even monophyletic with the Central African *Astylosternus* species.

The genus, as so far understood, offers no specific characters (Amiet 1977). All species have reduced webbing and toes II–V with terminal phalanges that may penetrate through the skin

(“cat claws”; compare Blackburn *et al.* 2008; Barej *et al.* 2010). The tip of the first toe is bent and all species have conspicuous interorbital patterns (Amiet 1977). Phalanges used for defense (Mertens 1938; Perret 1966; Blackburn *et al.* 2008) is a character also present in the closely related genus *Trichobatrachus* (Barej *et al.* 2010).

The known tadpoles of West and Central African *Astylosternus* are almost identical, being typical river tadpoles, with non-specialized mouth-parts (Angel 1930; Lamotte & Zuber-Vogeli 1954; Amiet 1977; this study). The more or less elongate body, a massive, muscular tail axis and narrow fins (Angel 1930; Lamotte & Zuber-Vogeli 1954) are adaptations to strong currents in the larval habitat. The similarly generalized labial-tooth row formulae and the massive jaw sheaths with serrated margins hint on a macrophagous diet on plant and/or animal matter. *Nyctibates corrugatus* larvae are superficially similar to *Astylosternus* tadpoles, concerning their general shape, (Amiet 1971). However, their body is even heavier, the lateral sacs more developed and they have different mouth parts, in particular almost reduced labial-tooth rows and very distinct upper and lower lips, indicating a food niche different to *Astylosternus* tadpoles (Amiet 1971). The closest relative of Central African *Astylosternus*, *Trichobatrachus robustus* (Frost *et al.* 2006; Pyron & Wiens 2011), has tadpoles with shorter bodies, a sucker mouth, narrower jaw sheaths, and many more labial tooth rows (Mertens 1938).

As our genetic analyses revealed that the genus *Astylosternus* might be paraphyletic, this implies that either *Trichobatrachus* Boulenger, 1900 needs to be sunk into *Astylosternus* Werner, 1898 or the West African *Astylosternus* would need their own genus. However, our data set, based on a comparatively small fragment of one mitochondrial gene, does not allow resolving this systematic problem. Because of the morphological and biological uniqueness of *Trichobatrachus*, in particular with respects to the “hairs” in breeding males, the reversed sexual size dimorphism (indicating special breeding behaviour) and the highly specialised tadpoles (Mertens 1938; Barej *et al.* 2010), we advocate to retain *Trichobatrachus*. However, we also do not believe that the detected genetic differences alone allow erecting a new genus for the West African “*Astylosternus*”. Their external adult and larval morphology fall well within the range of Central African species. We thus herein keep the West African frogs within *Astylosternus*, although being aware that the morphological similarity with Central African species might be due to convergent evolution of frogs in a similar habitat or plesiomorphic characters of the whole group, mainly comprising lentic species. The systematics within the family Arthroleptidae apparently need further investigation, in particular including anatomical and more molecular data. However, this was beyond the scope of this study.

The distribution of the two West African species is of biogeographic interest. Whereas *Astylosternus* are known from montane eastern Nigeria (e.g. Schiøtz 1963; Böhme & Nikolaus 1989; Lea *et al.* 2005; Reeder *et al.* 2011), numerous recent faunistic assessments have not revealed *Astylosternus* in any other area between the Cross River and the Volta River (Nigeria to Ghana, e.g. Eniang & Luiselli 2002; Lea *et al.* 2003; Rödel & Agyei 2003; Akani *et al.* 2004; Leaché *et al.* 2006; Rödel *et al.* 2007; Segniagbeto *et al.* 2007; Hillers *et al.* 2009; Onadeko & Rödel 2009), as well as between the Sassandra and Bandama Rivers in Ivory Coast (fig. 3.1.3-8). The distribution of the two West African species in the eastern (*A. laticephalus* sp. nov.) and western part (*A. occidentalis*) of the Upper Guinea forest zone is mirrored by i: the distribution of several other anuran species pairs, e.g. *Phrynobatrachus ghanensis* Schiøtz, 1964 / *P. guineensis* Guibé & Lamotte, 1962 “1961” (Zimkus *et al.* 2010); *Conraua derooi* Hulselmans, 1971 / *Conraua alleni* sensu lato Barbour & Loveridge, 1927 (Hulselmans 1971); *Hyperolius laurenti* Schiøtz, 1967 / *H. chlorosteus* (Boulenger, 1915) (Schiøtz 1999); ii: various fish and plant species (Falk *et al.* 2003; Poorter *et al.* 2004) and iii: the similarity of amphibian assemblages (Penner *et al.* 2011). Thus, the distribution of West African *Astylosternus* supports the hypotheses that a) rivers act as important zoogeographic barriers for amphibians in West Africa (Schiøtz 1967; Penner *et al.* 2011) and b) that smaller forests may have persisted as refugia for forest species during periods of climatic dryness, e.g. repeatedly during the Pleistocene (Haffer 1969; Maley 1996). During recurrent dry periods, African forests became islands surrounded by savannah (de Menocal 1995; Voelker *et al.* 2010). During more humid periods forests and their inhabitants expanded again. Most studies indicate that in West Africa such refugia may have existed in the region of the Nimba mountains (border between Guinea,



Liberia and Ivory Coast), and in south-western Ghana (Cape Palmas, Cape Three Points; e.g. Sosef 1994; Dupont *et al.* 2000; Falk *et al.* 2003; Poorter *et al.* 2004), thus reflecting the present day distribution of the two West African *Astylosternus* species. It is conceivable that isolated *Astylosternus* populations remained in eastern and western refugia during dry periods and there developed into the two species found today. After forests expanded again, the major West African rivers may have prevented new contact (fig. 3.1.3-8). Although it seems strange that species with larvae, well-adapted to fast flowing streams, are limited in their distribution by rivers, the separation of species with similar ecological requirements by a large river also explains best the distribution of the Central African *A. diadematus* and *A. batesi*, separated by the Sanaga River (Amiet 1977).

The discovery of *A. laticephalus* sp. nov. adds to the many anuran species already known to be endemic to the forests of eastern Ivory Coast and Ghana (Schjøtz 1999; Rödel *et al.* 2009a, b) and actually shows that the Upper Guinea hotspot (Myers *et al.* 2000; Bakarr *et al.* 2001) comprises at least two distinct hotspots of biodiversity richness, one in the forest of eastern Ivory Coast and Ghana and the other ranging from western Ivory Coast into Guinea, Liberia and Sierra Leone. Both areas, however, share the problem of intense forest fragmentation and conversion (Chatelain *et al.* 1996; Hillers *et al.* 2008c; Norris *et al.* 2010). Further efforts to assess and protect the unique biodiversity of West African forests thus remain an urgent task.



3.2 The uniqueness of West African amphibians

The delineation of geographic regions identifies unique areas and border/barriers to more different areas. West Africa was and is often seen as a part of Central Africa. In the following we provide a definition of the West African biome, based on amphibian data across the continent.

3.2.1 A hotspot revisited - a biogeographical analysis of West African amphibians

3.2.1.1 In a nutshell



The study was aimed at testing whether West Africa can be regarded as a distinct biogeographic region based on amphibian assemblages. If so, we asked what were the relationships of these assemblages with those in Central Africa, and whether West African amphibian distributions showed biogeographic substructure. We further investigated what events or processes may explain the observed patterns.

Location - Sub-Saharan Africa.

Presence-absence data of amphibian assemblages derived from field surveys and the literature were statistically analysed using three different multivariate techniques (consensus clustering, Monmonier analysis and nonmetric multidimensional scaling) to emphasize consistent results.

We showed that West Africa has unique amphibian assemblages, which could be clearly demarcated from Central African assemblages, particularly by the geographic barrier of the Cross River. Further biogeographic subdivisions were detected to the west of this barrier. Habitat, mainly forest, was the best factor explaining our observed pattern. Overall, intra-regional similarity (e.g. within West Africa) was higher than intra-habitat similarity (e.g. within forest) across regions.

Our results are compared with previous works and interpreted in the light of the known evolutionary history of West and Central Africa. The observed pattern may be explained by postulated differences in river continuity through time, with West African rivers serving as more or less constant barriers in contrast to those in Central Africa. Our results demonstrate the uniqueness of West African amphibian assemblages, highlighting the need for their conservation as many are under acute anthropogenic pressure.

3.2.1.2 Introduction

The delineation of biogeographical units has puzzled scientists for more than two centuries (Lomolino *et al.* 2004). Among the major scientific aims of biogeography remain the description and explanation of faunal and floral distribution patterns, as well as the identification of centres of high species richness and/or endemism. In Africa, as elsewhere, existing areas of high biodiversity have probably persisted during periods of extensive environmental change, e.g. glacial periods. They are, at least in part, considered to have served as Pleistocene refugia (e.g. Diamond & Hamilton 1980; Crowe & Crowe 1982; Mayr & O'Hara 1986; Grubb 1992).

Biomes with a high endemism and/or numbers of threatened species are of special conservation interest, resulting in the identification of 'hotspots', places of elevated endemic and threatened biodiversity. The original hotspot concept was based mainly on data from vascular plants and selected terrestrial vertebrates (Myers 1988, 1990; Myers *et al.* 2000). This global approach currently recognizes eight hotspots in Africa, of which the 'Guinean Forests of western Africa' is one. Similar 'hotspot' concepts have been applied in Africa for vascular plants (e.g. Linder 2001; Küper *et al.* 2004) and selected animal groups, such as mammals (e.g. Kingdon 1990; Kreft & Jetz 2010), birds (e.g. Crowe & Crowe 1982; De Klerk *et al.* 2002) and fishes (e.g. Roberts 1975; Hugué & Lévêque 1994) but see e.g. Kareiva & Marvier (2003) for criticism of the concept. Recent collaborative studies have combined a number of different vertebrate taxa



(mammals, birds, snakes and amphibians) in order to identify areas in Africa containing high biodiversity (see Hansen *et al.* 2009 for a comprehensive list of publications). Conservation biologists are embracing biogeographical research in response to the steadily growing human-induced pressures on biodiversity, as well as dwindling conservation resources such as financial and human capital. As a consequence, conservation efforts have to be directed and channelled necessitating hard choices concerning threatened sites and species (e.g. Brooks *et al.* 2006; Wilson *et al.* 2006, 2009; Carwardine *et al.* 2008; Underwood *et al.* 2008). Consequently, it is necessary and enlightening to relate patterns of diversity not only to biogeography, but also to phylogenies and conservation, environmental, and/or social variables.

Mostly because of the limitations of data availability, many previous studies identified particular hotspots based on a coarse geographic scale, e.g. grid cells of 1°, c. 111 x 111 km at the equator. However, in general, areas used for conservation planning are much smaller (Shriner *et al.* 2006), and although conservation planning, such as priority setting, can be derived from large scales (Larsen & Rahbek 2003), a finer resolution often achieves better results (Warman *et al.* 2004; Hurlbert & Jetz 2007; Jetz *et al.* 2007). Although most countries have a conservation network with at least some kind of legal status, gaps in space and taxa remain. It is frequently suggested that these gaps should be closed, but final selection criteria for decision makers are manifold and often include economic priorities. Many protected areas in Africa, for example, are located in less fertile regions, or have other limitations that prevent human settlement or agriculture, e.g. diseases or parasites (Ford 1971). Whether existing protected areas effectively cover areas of high biodiversity often remains untested, and the knowledge to prioritise areas based on, for example, postglacial colonization routes, historical refugia, barriers, and/or biogeographic units is scarce.

A variety of taxa have been used to approach such questions. Among vertebrates, amphibians have experienced the highest increase in species with Red List status during the last decades (Stuart *et al.* 2008). Although this could be because of a hidden bias, as complete assessments for fish and reptiles are lacking. In part, their vulnerability stems from the comparatively high habitat specificity of many species and their low mobility. Currently, more than 30% of all amphibian species are threatened and included on the Red List, making amphibians one of the most threatened class of organisms world-wide (Stuart *et al.* 2004). The main threats are habitat destruction and alteration (e.g. Stuart *et al.* 2008), and this situation may become worse if forecasted climate changes are correct (Carey & Alexander 2003; Corn 2005; Araujo *et al.* 2006). The combination of habitat specificity, low mobility, and ease of sampling of the group in a standardized manner makes it an ideal biogeographical model group (Zeisset & Beebee 2008).

For Africa, the highest regional amphibian diversities have been mapped for the Cameroon Highlands and for the 'Eastern Afrotropical hotspot' (see Hansen *et al.* 2009). In these and other publications, West Africa (WA) is frequently also considered a hotspot, although often, either directly or implicitly, regarded as being a subset of the Central African (CA) bioregion (see review by Werger 1978). For example, Poynton (1999) in a continental analysis of amphibian biogeography stated '... part [of West Africa] could be regarded as a subtraction margin of the fauna of Cameroon.' In this analysis, the whole 'west equatorial' region was subdivided into four blocks: central, south, east and west, the latter comprising WA west of the Dahomey Gap. In another study, Schiøtz (1967) analysed the distributions of reed frogs (Hyperoliidae) and other selected amphibian taxa and identified major zoogeographical barriers in WA by comparing visually the detected barriers to distributions of mammals (mainly primates) and birds. Two main barriers were confirmed: the Dahomey Gap and the Cross River. Throughout these and other studies (cited earlier), the exact delineation of WA biogeographic units with respect to CA appears to be haphazard. This stimulated us to pose four questions that we addressed using a data set of African amphibian assemblages. First, we tested whether a distinct WA bio-region could be defined, or whether the region was a subset of the CA bio-region. Second, if WA was shown to contain unique assemblages, we asked where the boundary between the CA bio-region was geographically located. Third, we examined whether WA displayed sub-regions, comprising smaller, but distinct biogeographical units. Finally, we analysed which factors could

cause the observed biogeographic pattern. The overarching goal behind these questions was to discover regions that may require specific conservation measures.

3.2.1.3 Methods

3.2.1.3.1 Geography and data set

Our study is confined to mainland sub-Saharan Africa. Data on 120 amphibian assemblages have been compiled through our own field surveys (65 sites) and from literature records (55 sites). Species taxonomy was harmonized (see app. 3.2-1). Literature records have been updated to current taxonomy, and when necessary checked for plausibility. The genus *Arthroleptis* has been omitted because of the unresolved taxonomic status of most WA taxa (Rödel & Bangoura 2004). In addition to the presence of a species at a particular site, the following information was noted (after IUCN 2010): Red List status, presence between our postulated barriers (see section on causes for delineations), irrespective of the database record and habitat preferences (see the following paragraphs for details). The final data set comprised binary data for a total of 528 species (3161 presence records). Country codes throughout the text follow ISO standards (ISO 3166-1 accessed 11th January 2010). Ideally, rarefaction curves or estimators should be used to assess the sampling efficiency of each site and to estimate its alpha diversity (Magurran 2004). However, our data set did not allow for that, because seasons and survey designs differed considerably between sites and some literature records did not contain the necessary information (e.g. daily species lists and sampling effort). Despite these caveats, analyses can be adjusted to presence/absence (binary) data, and these analyses achieve similar result to abundance-based analyses (Furse *et al.* 1984; Marchant 1990).

3.2.1.3.2 Delineation of WA amphibian assemblages

Our first question was whether WA has unique amphibian assemblages, i.e. if they are more similar to each other than to other assemblages on the continent. This question can be addressed if there is either a gradual change in assemblage similarity, or a clear cut boundary with respect to CA assemblages. In the latter case, we investigated where this boundary or barrier is geographically located.

Binary data of all amphibian assemblages were translated into three dissimilarity matrices using three different indices. The choice of indices is crucial as it heavily influences further analyses (e.g. Learner *et al.* 1983; Legendre & Legendre 1998), and there is a multitude (over 80) of different indices plus transformations, although the use of binary data limits this choice. It is important to weigh the alternate states, presence/absence, differently (Legendre & Legendre 1998), as absences are more difficult or even impossible to ascertain (e.g. Kéry 2002) and thus presence data are more informative. However, there is no agreement on how to weigh the two different states, and there is no single index that is solely recommended. Consequently, we chose three indices that are well suited for binary data and vary in the weights given to the two states.

Jaccard (1908) – is the simplest index (Legendre & Legendre 1998) and is often used for binary data and can therefore be easily compared with other studies. It is calculated as the number of shared species divided by the number of shared species, plus the number of singletons (species recorded in only one assemblage). To use it as a dissimilarity index, the formula has slightly been modified, using the Bray–Curtis dissimilarity (Oksanen 2008). Its major disadvantage is its sensitivity to sample size (Oksanen 2008), thus making it difficult to compare assemblages with very different species richness or different sampling intensities.

Mountford (1962) – the advantage of this index is that it is less sensitive to different sample sizes. It is derived from Fisher's log series. There are several disadvantages; it is not commonly used, and the index is non-metric (Shepard 1984; Oksanen 2008) which means that there is no linear relationship within the index itself.



Raup & Crick (1979) – is also a non-metric index and a measure of the probability of observing the same species in the compared assemblages. The probability is derived from a hypergeometric distribution (Legendre & Legendre 1998). Absent species from two compared assemblages are weighted more strongly than in the other two indices (Oksanen 2008).

The consensus of the three indices allows for more robust conclusions, and the emphasis in our study was placed on consistent results, although different methods were applied. Using these three indices, we gained three dissimilarity matrices for the 120 assemblages. To uncover potential general geographic patterns, we used a Mantel test to test whether sites close to each other had more similar assemblages than sites at a greater distance. The test searches for correlations between geographic distances (Euclidian distances) species compositions. However, the test does not categorize assemblages according to their similarities. For that we grouped assemblages via cluster analyses, using the dissimilarity matrices as distance measures. A variety of different linkage methods are available (e.g. Leyer & Wesche 2007; Mouchot *et al.* 2008) and groupings are strongly dependent on the distance measures as well as the cluster criteria used (Gordon & Vichi 2001). Consequently, we again applied the consistency (consensus) principle. If groups were detected consistently by different indices and different methods, we considered them as being well supported (Leyer & Wesche 2007). As we aimed at avoiding any presumptions on the number of groupings, we employed hierarchical clustering. We used an optimization approach to construct a final single cluster. As a result, 21 clusters were combined, i.e. we combined three distance measures (Jaccard, Mountford, Raup-Crick) and seven linkage methods [single linkage (nearest neighbour), complete linkage (furthest neighbour), average linkage (UPGMA), median linkage (WPGMC), centroid linkage (UPGMC), McQuitty's method and Ward's method; see Sneath & Sokal 1973 for details]. The chosen linkage methods differed in their grouping properties, meaning that they either tended to build single similarly sized groups (single linkage), few large groups (complete linkage) or behaved neutral (conservative, all other linkage methods). When minimizing Euclidian dissimilarity (Hornik 2009), a single consensus cluster was gained. Agreements between pairs of clusters were calculated as one minus the rate of inversions between associated ultrametrics (Hornik 2009).

The above cluster analysis groups assemblages but does not take their spatial array into account. Therefore, assemblages might be grouped close to each other, although they are geographically separated by large distances. This hampers biogeographical explanations, especially if assemblages containing different amphibians are located between them. One way to include information on the geographic location of an assemblage is to use the Monmonier algorithm (Monmonier 1973). Here, assemblages are first directly connected in a geographic space (Delauney network). Subsequently, a boundary orthogonal to the connecting line is drawn in the middle between two assemblages. This procedure is conducted from every assemblage towards every neighbouring assemblage (Voronoi tessellation; see Dupanloup *et al.* 2002; Manni *et al.* 2004; Jombart, 2008). Subsequently, the algorithm searches homogenous areas and delineates them towards other areas. Barriers are drawn on the orthogonal boundaries in order of their significance, starting with the most significant one. Hence, geographical boundaries are depicted between the most dissimilar assemblages that are geographically close.

It is important to evaluate whether most known species are listed for a specific region because generally species that remain undetected may have a negative impact on statistical analyses. Thus, species richness estimations of regions were calculated as rarefaction curves for the whole continental data set and for the speculated WA subset. Rarefaction adds numbers of species per site cumulatively. The order of sites is randomly arranged and the process iterated, leading to a smoothed average of all curves. When this smoothed curve reaches a plateau, it is likely that most species have been recorded (Sanders 1968; Hurlbert 1971; Simberloff 1972). However, no extrapolation on the number of expected species can be made (Bush *et al.* 2004).

3.2.1.3.3 Causes for the delineations

Monmonier analysis, as described earlier, draws the location of the barriers always in the middle between two assemblages. This is independent of geographic features on the ground. Rivers especially are often neglected as barriers though their function is confirmed for amphibians (Li *et al.* 2009) and even large mammals (Anthony *et al.* 2007). To test specific barriers, we hypothesized nine potential barriers based on altitude, river systems, floral regions (Udvardy 1975; White 1983; Olson *et al.* 2001) and previous work on amphibians (Schlötz 1967, 2007; Poynton 1999). Specifically, we tested the following barriers (from east to west): Cross River, Niger River, the Dahomey Gap, Volta River (now Lake Volta), Banadama River (which continues in the rain forest zone as a v-shaped gap, called V Baolé), Cavally River (including the Upper Guinea highlands), Mano River, Kolente' River (including the Fouta Djallon) and Géba River (see fig. 3.2.1-1).

To assess which factors are responsible for the observed distribution patterns, three types of information have been added for each species: (1) a simple ecological classification, detailing whether the species occur in forest, farmbrush, woodland, savannah, montane grasslands or fynbos (after IUCN 2010; compared with fig. 3.2.1-2; multiple allocations were allowed); (2) nine potential biogeographical barriers dividing the species' ranges into ten potential partitions. A third category, (3) IUCN Red List classification (app. 3.2-1), was also added to detect where threatened assemblages occur and how they are potentially related to biogeographical patterns. The threat status was also weighed, either linearly (NL = 2; DD = 2; LC = 1; NT = 3; VU = 4; EN = 5; CR = 6) or exponentially (NL = 2; DD = 2; LC = 1; NT = 4; VU = 8; EN = 16; CR = 32), to emphasize higher threat categories.

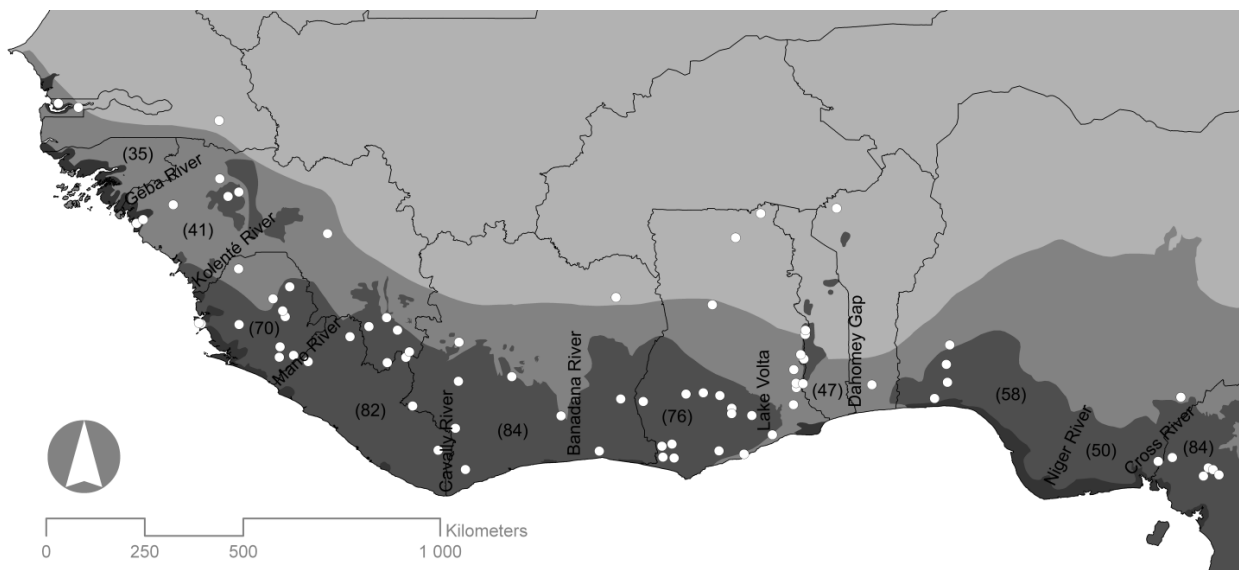


Fig. 3.2.1-1: Map of West Africa (World Cylindrical Equal Area Projection). White circles indicate the sites of our amphibian assemblage data. Names indicate the rough location of the potential faunal barriers. Numbers in brackets show the number of species between the bordering barriers. Landscape characteristics are simplified from the WWF ecoregions (Burgess *et al.*, 2004) to indicate ecological zones, and are coded (south to north, dark grey to light grey): mangrove forests; lowland forests; forest-savannah transition zone; savannah.

To test the influence of these factors, habitat, barriers and threat status, non-metric multidimensional scaling (NMDS) was used. This is an iterative optimization procedure and is preferred over similar techniques, e.g. principal component analysis, because it is flexible and has no underlying assumptions, such as linear relationships or parametric data (Kruskal & Wish 1978; Clarke 1993). This indirect gradient analysis results in a reduction to a few dimensions, or axes, on a real or hypothetical environmental gradient. No real environmental data of the sites is recorded for this analysis. To avoid the statistical problem of the analysis getting 'trapped in local optima' (McCune & Grace 2002), the NMDS was repeated 10.000 times per run. The



NMDS places the sites into an n-dimensional space, n being the number of factors included. Factors, habitat, occurrence within hypothesized barriers and red list classification were fitted as new axes and therefore as explaining vectors for the observed pattern. All analyses were conducted with the software R 2.9.0 (2009) using the packages 'Adegenet', 'Clue', 'Mass', 'Stats' and 'Vegan 1.15-2'.

3.2.1.4 Results

Overall, 120 amphibian assemblages have been analysed, comprising a total of 528 species (app. 3.2-1). Total species richness and richness for all sites is actually higher, as the genus *Arthroleptis* has been omitted (see Methods). Our main question was whether there are distinct amphibian faunal regions. A first Mantel test for all African assemblages confirmed that amphibian assemblages in close geographic proximity have a higher similarity than assemblages in greater distance ($P < 0.001$). In a second step, we examined whether this pattern remained on a regional scale.

Consensus clustering grouped amphibian assemblages close to each other according to their faunal similarity (fig. 3.2.1-2). The congruence between the 21 different groupings (three similarity indices multiplied by seven linkage methods) was 68%. Within the derived single consensus tree, one single central cluster was obvious. It contained only sites west of the Cross River which is roughly the border between Nigeria and Cameroon. The right column of the graph shows this graphically (fig. 3.2.1-2). The lengths of the bars indicate species richness, and colours indicate to which region the assemblage is allocated. Based on our results WA, the green group, is herein defined as the region west of the Cross River and south of the Saharan desert. Hence, Nigeria is included and Cameroon excluded. Two further distinct clusters are apparent. The first one (bottom) groups East and Southern Africa. Two assemblages from Congo (CD) were embedded within this group. The second cluster comprised all remaining CA assemblages. Habitat preferences for all recorded species are depicted in six classes (middle section of fig. 3.2.1-2). Interestingly, WA savannah and rain forest assemblages were more similar to each other than rain forest assemblages of WA and CA or savannah assemblages in general. However, within the large WA cluster, rain forest and savannah assemblages grouped separately.

Of the 528 species, 172 were recorded in the WA cluster. Slightly more than 50% occurred only there (90 species). In WA, 22 species were only represented in one single assemblage. On a continental basis, three regions in Cameroon were the most species rich (Mt. Nlonako, Korup, Nkongsamba). Similar rankings were observed for genus richness (Korup, CM; Mt. Nlonako, CM, Mt. Doudou, GA). Family richness was highest in sites in Gabon and Tanzania (Mt. Doudou, GA; Mahenge, TZ; Usambara Mts., TZ; Crystal Mts., GA). Rankings remained the same when all taxa of unresolved taxonomy were excluded from the analysis. Highest numbers of such taxa were noted in CA (Mt. Doudou, GA; Mt. Manengouba, CM; Korup, CM; Tchabal, CM). Within the WA cluster, the assemblages of Mt. Nimba (CI, GN, LR), Pic de Fon (GN) and the Taï National Park (CI) were the taxa richest. The species-richest sites also contained the highest numbers of threatened species (Spearman's rank correlation test, $P < 0.001$). Thus, the top ranking sites kept their status when species occurrences were weighed by threat status. Exponential weights changed the order slightly, by putting more emphasis on three sites, i.e. Obudu (NG), Ankasa and Atewa (both GH; see app. 3.2-1).

Rarefaction results have to be treated carefully. Comparisons between all assemblages, the WA ones and the cumulative number of species were conducted. In the latter, the sites were ranked geographically from the west to the east and to the south (fig. 3.2.1-3). The boundaries between regions can be identified by a sharp increase in the cumulative number of species. The comparatively flat rarefaction curve for WA confirms that this region is better represented in our database than the whole continent. More generally, the flat curve shows that for WA, most species are present in the database; only three valid species are missing *Amietophrynus danielae*, *Amietophrynus perreti*, *Phrynobatrachus brongersmai*.

As the cluster analysis does not take into account the geographic relationships of the assemblages, a Monmonier analysis was conducted, searching for differences between neighbouring assemblages. The analysis partly supported the proposed barriers. In particular, it confirmed the Cross River as dividing the West from the CA amphibian assemblages. Furthermore, the analysis confirmed the Kolenté River and the Lake Volta as separating distinct groups of species assemblages within WA. Between these two rivers, we detected the assemblages with the highest number of species in WA. To reveal the finer structure within the WA data set, the Monmonier analysis and ordination were conducted for the WA assemblages only ($n = 74$).

The NMDS analysis also clearly separated WA from all other assemblages (stress values for the 3 dissimilarity measures used: Jaccard 20.73, Mountford 22.31, Raup-Crick 20.46). Within WA, species occurrences between the hypothesized barriers proved to be significant and therefore not randomly structured (app. 3.2-2 & 3.2-3). Nine geographic partitions were highly significant ($p < 0.001$) throughout all used dissimilarity measures. The other partitions also showed varying degrees of significance (app. 3.2-2). The major factor responsible for the groupings within WA is the habitat specificity of the species. Assemblages dominated by forest and farmbrush species separate well from assemblages containing mostly savannah and woodland species (app. 3.2-2). The IUCN Red List status also differentiates assemblages (app. 3.2-2). This is because of a correlation between Red List status and habitat preference, threatened species being predominantly found in threatened habitats, e.g. forests and montane grasslands.

In a nutshell, our results show that WA amphibian assemblages are unique compared with other African assemblages. Several geographic partitions have been indicated and the Cross River has been confirmed as the major barrier towards CA. Explanatory variables are multifaceted, with species habitat preferences being dominant.

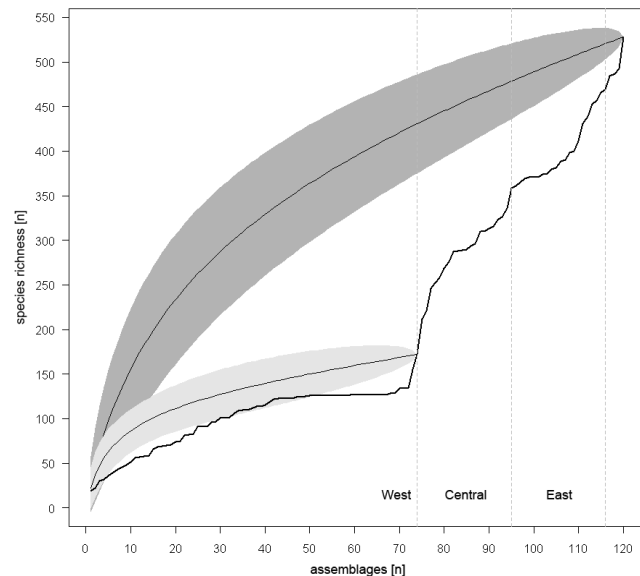


Fig. 3.2.1-3: Rarefaction curves and standard errors of cumulative species richness for all (dark grey) and West Africa only (light grey) assemblages. The bold line cumulatively records species richness sorted geographically from west, central, east and south (the latter, because of limited sites, not labelled in the figure). Large steps in the slope indicate biogeographical boundaries. Dashed lines indicate tentatively major boundaries.

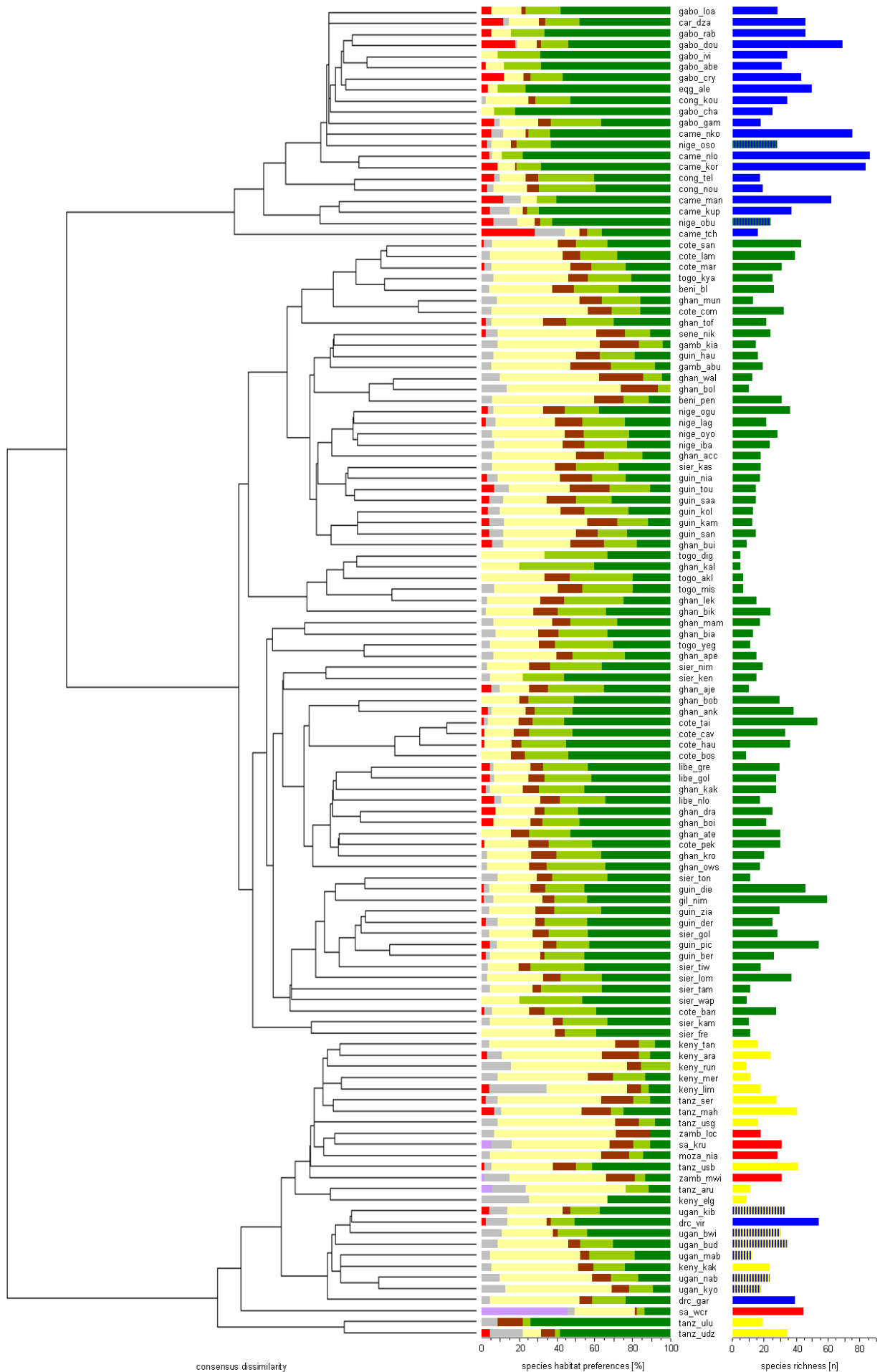


Fig. 3.2.1-2: Consensus cluster of 120 African sites depicting similarities in their recorded amphibian assemblages. West African amphibian communities group together and can be further divided into rain forest and savannah sites. The central panel of bars show the proportions of species habitat preferences (dark green = forest, light green = farmbush, brown = woodland, yellow = savannah, purple = fynbos, grey = montane grassland, red = not assigned). Bars on the far right indicate absolute species richness (length) and the African region (green = west, blue = central, yellow = east, red = south; striped communities can be assigned to two regions).

3.2.1.5 Discussion

Two of the most important aims in conservation are to protect species and sites. Certainly, the best strategy is to preserve species in their natural habitats. Therefore, it is vitally important to know where unique areas are located, e.g. in terms of rare and unique species, and how these areas can be delineated. To reveal such delineations in Africa, several attempts with different definitions using different organisms have been put forward and discussed (see introduction). Our study is the first comprehensive analysis of WA amphibian assemblages, showing that this region has unique species compositions compared with other African realms. This is due to the fact that a large number of species occur only in WA. Previous works on amphibians (Schlötz 1967; Poynton 1999) did suggest the Cross River as important geographic barrier for species distributions, but did not weigh it against other barriers. They did also detect another clear-cut species boundary in the western part of the region, the Mano River approximately on the border between Liberia and Sierra Leone. However, our analyses did not confirm the Mano River as a very sharp boundary and other barriers within the WA region were also not prominent, e.g. by marked drops in species diversity, as previously suggested. This is probably due to two facts: first, the areas 'outside' the barriers, e.g. west of the Mano River, are climatically suitable for forest (Harcourt *et al.* 1992) and therefore provide suitable habitats for many species. Second, Guinea and Sierra Leone have not been studied formerly in detail and this is the first time that recent and detailed amphibian surveys of these countries have been included in biogeographic analyses. Several other biogeographic studies (see Introduction) focused on mammals and plants in the region. Most did not reveal the Cross River as the delineation between WA and CA bio-regions, and usually placed emphasis on the Dahomey Gap or the Niger River. However, two exceptions exist, i.e. studies on bushbucks (Moodley & Bruford 2007) and duikers (Colyn *et al.* 2010), which both detect a clear difference in genetics and morphology between species on either side of the Cross River.

The factor consistently explaining the division of WA towards CA and the subdivisions within the region is habitat; 'forest' assemblages are especially unique. It is important to note that many WA amphibian species occur only in primary (= undisturbed) and not in disturbed forests (Ernst & Rödel 2005; Ernst *et al.* 2006; Hillers *et al.* 2008c). Beside forests, montane grasslands likewise had a large impact on the clustering of assemblages, as this rare WA habitat is home to many specialized species.

In addition to the inter-regional and well-defined WA and CA assemblages, separated by the Cross River, an intraregional grouping by habitat is evident in WA. Thus, within the WA region, two major groups of amphibian assemblages could be identified: forest and savannah assemblages. That intraregional grouping by habitat is not as distinct as that by region may have several explanations. One is the way in which species habitat preferences is recorded, as some species occur in more than one habitat type. Thus, similar assemblages may comprise species of differing habitat preferences. Additionally, there is no sharp boundary between forest and savannah biomes but rather a broad transition zone (see White 1983; Burgess *et al.* 2004). Assemblages located in the transition zone are more likely to contain higher percentages of species from both habitat types, compared with assemblages from very distinct habitat zones. This gradual change in biomes is partly reflected in the composition of WA amphibian assemblages. Another reason is that most forests in WA are severely fragmented and threatened (Achard *et al.* 2002), and within the true forest region, new habitats are anthropogenically generated. These generally favour savannah species, enabling the invasion of farmbush and savannah species into assemblages that would naturally feature a higher percentage of true forest species.



The origin of anurans, comprising the vast majority of our taxa, is dated to the beginning of the Triassic (ca. 250 Ma; e.g. Roelants *et al.* 2007). African anurans might have evolved later, around 100 Ma (see Zimkus *et al.* 2010 and references therein). Recent speciation pulses have occurred c. 15–10 Ma ago (review in Moritz *et al.* 2000; Wieczorek *et al.* 2000; Zimkus *et al.* 2010). However, these dates have to be treated with caution as no data on WA amphibian fossils exists to root these phylogenetic trees. Also information on the WA climate beyond the last glacial maximum (> 20.000 years) is generally meagre. Hence, comparisons between the evolution of the WA amphibian taxa and the evolution of the observed biogeographic pattern under palaeo-climate scenarios are difficult. A more interesting question is why WA forest and savannah assemblages form a cluster separate from CA forest and savannah assemblages. In general, three hypotheses may apply. Species may have evolved along an ecological gradient (Endler 1982; Fjelds  1994), in riparian refugia (Colyn *et al.* 1991; Aide & Rivera 1998) or in refugia of climatic stability (e.g. Diamond & Hamilton 1980; Crowe & Crowe 1982; Mayr & O'Hara 1986; Grubb 1992). If, as is commonly suggested, the evolutionary history of both regions was more or less the same, inter-regional similarity of savannah dominated assemblages should be higher as no WA–CA barrier is commonly suggested for the savannah region. This suggests that the evolutionary history differs between the regions. A possible scenario is that forest and savannah assemblages in WA have evolved together. The main driving force for this co-evolution could have been substantial expansions and contractions of forest extents between and during the ice ages (Hamilton 1976; Maley 1996). Thus, WA assemblages might have evolved in a mosaic landscape, with cyclical fragmentation and re-connecting of forest and savannah patches. As a result, forest and savannah assemblages evolved in close proximity and species exchanges were likely. In contrast, CA assemblages might have evolved in a situation where forest and savannah blocks retained greater connectivity. As a consequence, the habitat assemblages may have evolved more separately. However, it is often suggested that forest remnants in CA were minute (Amiet 1987; Hamilton & Taylor 1991; Maley 1996). A model for forest–savannah mosaic in dry periods has been discussed for plants and primates in the Congo Basin (Colyn *et al.* 1991), but this remains controversial and it has not been applied to WA. Overall, the question exactly how forests were expanding or shrinking during different climatic periods remains open. The CA forests could have remained more or less stable throughout time and without change, as has been hypothesized for the Eastern Arc Mountain forests (Finch *et al.*, 2009; but see discussion therein).

In this respect, two other differences between WA and CA are notable, potentially explaining the uniqueness of WA assemblages. First, around 54–49 Ma ago, several 'bizarre pollen types' appeared in CA only (Morley 2000). The identification of the plants associated with these pollens, and the ecological changes associated with their appearance, remains unknown. They may represent the traces of unique habitats that occurred only in CA, and were absent in WA. Later, when the species assemblages of both regions had diverged, the unique habitats in CA were replaced by similar habitats in both regions. Alternatively, hydrological features in WA have remained more or less consistent since the Miocene (23–5 Ma; John 1986). This coincides, for example, with the diversification of *Hyperolius* and *Phrynobatrachus* species during the late Oligocene, early Miocene (Wieczorek *et al.* 2000; Zimkus *et al.* 2010), and probably other amphibians as well (see review by Moritz *et al.* 2000). Rivers probably broadened during wet periods (Nicolas *et al.* 2008), thereby increasing their effectiveness as barrier. This contrasts with the biogeography of eastern Africa, where the recent hydrological system is much younger (John 1986). The hydrological history of CA is less clear. It is speculated that the Congo River may have been unconnected to the ocean until 30 Ma ago (review by Goudie 2005) and therefore did not act as a barrier in western CA. In these hydrological models, the WA amphibian assemblages may have been 'trapped' between river barriers, resulting in regional similarity despite the presence of the major forest and savannah habitats. In contrast, continuous exchange within habitats was possible for most of this period for CA assemblages.

Areas with a high biodiversity are often equated to areas where Pleistocene refugia may have been located. Previous work (see introduction) on the location of these refugia has yielded conflicting results. Generally, three WA refugia have been postulated. The first contains south-

eastern Liberia and south-western Côte d'Ivoire, including Mt. Nimba, although the latter may have also been a separate refuge. This whole area is also often called 'Upper Guinea'. The second refuge has been thought to be located between south-eastern Côte d'Ivoire and south-western Ghana. The third refuge belongs to CA but stretches partly into the far south-eastern tip of Nigeria and includes areas west of the Cross River (see fig. 3.2.1-1; Maley 1996). The exact delineation of these refugia remains imprecise and varies between authors, e.g. the forest block ranging from the Taï National Park in Côte d'Ivoire through to the Liberia-Sierra Leone border, may have acted as one single Pleistocene refugium (Laurent 1973). This block is often considered a single ecoregion (Burgess *et al.*, 2004), and the rough position, extent and entity of this potential forest refugium has been supported in various studies (e.g. Chapman 1983; Mayr & O'Hara 1986; Brooks *et al.* 2001; De Klerk *et al.* 2002; Küper *et al.* 2004). Using geomorphology derived from satellite imagery, Nichol (1999) likewise showed only one forest block as a historical refuge, but placed it slightly further to the northwest. Our results suggest that this single block can probably be divided into at least two refugical blocks based on similar amphibian assemblage. One covers the area around the Taï National Park in Côte d'Ivoire, and the other an area in south-western Sierra Leone. Although the Mano River may act as the barrier between these refugia, the scale of our analyses and the little data available for Liberia do not allow more precise positioning.

We report a clear distinction of WA amphibian assemblages from those of other African regions (central, eastern and southern Africa). Within WA, the intra-regional change in similarity of amphibian assemblages is gradual west of the Cross River. The latter is the most prominent and distinct barrier clearly delineating the hotspot 'Guinean forests of West Africa' from those in the east. Several other barriers of lesser importance structure the assemblage composition within WA.

Our analyses do not allow any firm conclusions on barriers between the other large African regions (east, south & central). Judging from the rarefaction results, where the cumulative number of species increases from region to region and sudden slopes indicate sharp transitions, one could speculate that a sharp boundary between east and southern Africa does not exist. This combined region is differentiated from that of CA by having an 'arid corridor' that ranges approximately from the Horn of Africa to the Cape of Good Hope (Balinsky 1962; Poynton 1995). Herpetologically, this disjunction is supported by data from hyperoliid frogs (Seymour *et al.* 2001) and reptile assemblages (Wagner *et al.* 2008).

Our demonstration of the uniqueness of WA amphibian assemblages shows that specific conservation plans are needed for WA. These should prioritise mainly the area between the rivers Volta and Kolenté. This is the most species rich and consequently outstanding area in WA. In addition, it contains a high number of threatened and endemic species. Within this area, amphibian assemblages of two sites are outstanding: Mt. Nimba and the Taï National Park. The former contains mountain grassland habitat, which is very rare in WA: the latter comprises the largest protected lowland rain forest in WA. Both sites are threatened by anthropogenic activities, i.e. mining (Hillers *et al.* 2008d) and logging (Hillers *et al.* 2008c), respectively. Their surroundings already comprise highly fragmented forest, or are now cleared of forest (Chatelain *et al.* 1996; Mayaux *et al.* 2004), which places further pressure on the fragments.





3.3 Threats - the case of the Chytrid fungus

Numerous threats are a hazard for amphibian populations worldwide. Diseases play an important role, besides habitat destruction and alteration. In the following I discuss the case of the chytrid fungus from an African perspective.

3.3.1 West Africa - A safe haven for frogs? A sub-continental assessment of the chytrid fungus (*Batrachochytrium dendrobatidis*)

3.3.1.1 In a nutshell



A putative driver of global amphibian decline is the panzootic chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*). While *Bd* has been documented across continental Africa, its distribution in West Africa remains ambiguous. We tested 793 West African amphibians (one caecilian and 61 anuran species) for the presence of *Bd*. The samples originated from seven West African countries - Bénin, Burkina Faso, Côte d'Ivoire, Ghana, Guinea, Liberia, Sierra Leone - and were collected from a variety of habitats, ranging from lowland rainforests to montane forests, montane grasslands to humid and dry lowland savannahs. The species investigated comprised various life-history strategies, but we focused particularly on aquatic and riparian species. We used diagnostic PCR to screen 656 specimen swabs and histology to analyse 137 specimen toe tips. All samples tested negative for *Bd*, including a widespread habitat generalist *Hoplobatrachus occipitalis* which is intensively traded on the West African food market and thus could be a potential dispersal agent for *Bd*. Continental fine-grained (30 arc seconds) environmental niche models suggest that *Bd* should have a broad distribution across West Africa that includes most of the regions and habitats that we surveyed. The surprising apparent absence of *Bd* in West Africa indicates that the Dahomey Gap may have acted as a natural barrier. Herein we highlight the importance of this *Bd*-free region of the African continent - especially for the long-term conservation of several threatened species depending on fast flowing forest streams (*Conraua allenii* ("Vulnerable") and *Petropedetes natator* ("Near Threatened")) as well as the "Critically Endangered" viviparous toad endemic to the montane grasslands of Mount Nimba (*Nimbaphrynoides occidentalis*).

3.3.1.2 Introduction

Amphibian populations are declining in many regions of the world (Stuart *et al.* 2008). This is due to a number of causes. Besides the main contributors, like destruction, alteration and fragmentation of habitats, an often suggested cause is a fungal pathogen of the order Chytridiales (*Batrachochytrium dendrobatidis* Longcore *et al.*, 1999 - hereafter referred to as *Bd*) which induces the disease chytridiomycosis. The link between declining populations and *Bd* has been subject to a number of reviews (Daszak *et al.* 1999, 2003; Skerratt *et al.* 2007; Fisher *et al.* 2009; Kilpatrick *et al.* 2009; Heard *et al.* 2011; Wake 2012). So far it has been responsible for declines in Australia (Berger *et al.* 1998, 1999; McDonald & Alford 1999), New Zealand (Waldman *et al.* 2001), Central America (Crawford *et al.* 2010, Lips 1999; Young *et al.* 2001; Lips *et al.* 2004, 2006, 2008), North America (Bradley *et al.* 2002; Muths *et al.* 2003; Rachowicz *et al.* 2006) and Europe (Bosch *et al.* 2001). *Bd* has also been detected in many other regions (see Aansen 2011 for the most recent worldwide compilation), but not associated with declines.

Currently African records are widespread in southern and eastern Africa, including eastern parts of the Democratic Republic of Congo. These are complemented by very recent additions from Nigeria (Imasuen *et al.* 2009, 2011; Reeder *et al.* 2011), Cameroon (Baláz *et al.* 2012; Doherty-Bone *et al.* 2013) and Gabon (Bell *et al.* 2011) (fig. 3.3.1-1). So far no information has been reported about the pathogen's presence in West Africa. In addition to investigating the pathogen's presence with molecular or histological methods, we infer the likelihood of *Bd* occurrences using environmental niche modelling (ENM). ENM models the Grinnellian niche measured by scenopoetic variables (*sensu* Peterson *et al.* 2011). This tool has been shown to contribute significantly to our understanding of current species distributions (e.g. Franklin 2010;



Elith *et al.* 2011; Peterson *et al.* 2011) and has already been used to model the distribution of pathogens, including that of *Bd* (e.g. Ron 2005; Rödder *et al.* 2008, 2009, 2010; Puschendorf *et al.* 2009; Adams *et al.* 2010; Lötters *et al.* 2010; Murray *et al.* 2011). Potential distributions predicted by the models may then guide future surveys aimed at detecting the focal organism (e.g. Tinoco *et al.* 2009, Tittensor *et al.* 2009) and preventive measures.

Herein, we compare extensive field surveys for *Bd* based on samples from seven West African countries with results of detailed African continental ENMs, which include the most recent *Bd* positive records. Our findings are discussed with a special focus on common species and on species which are potentially highly threatened by the fungus because of their high niche overlap with *Bd*.

3.3.1.3 Materials and Methods

3.3.1.3.1 Ethics Statement

All work complies with the guidelines for the use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL) and the Society for the Study of Amphibians and Reptiles (SSAR). For ethical issues concerning the toe clips we refer to (Grafe *et al.* 2011), we followed recommendations therein.

Permits were issued by the respective companies, institutions, ministries as well as government bodies: Bénin - Faculté des Sciences Agronomiques, Département d'Aménagement et de Gestion de l'Environnement, Laboratoire d'Ecologie Appliquée, Université d'Abomey-Calavi on behalf of the Centre National de Gestion des Réserves de Faune and the Ministère de l'Environnement et de la Protection de la Nature; Burkina Faso - Unité de Formation et de Recherche en Sciences de la Vie et de la Terre, Département de Biologie et Physiologie Végétales, Laboratoire de Biologie et Ecologie Végétales, Université de Ouagadougou on behalf of the National Centre of Scientific and Technology Research of Burkina Faso; Côte d'Ivoire - Ministère de l'Environnement et du Cadre de Vie, Direction de la Protection de la Nature; Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, Direction de la Recherche; Ministère de la Construction et de l'Environnement, Direction de la Protection de la Nature; Ministère de l'environnement et de la Forêt, Direction de la Protection de la Nature; Société de Développement des Forêts; Ghana - Wildlife Commission of the Forestry Commission of Ghana; Guinea - Ministère de l'Agriculture, de l'Elevage, de l'Environnement et des Eaux et Forêts; Ministère de l'Education Nationale et de la Recherche Scientifique, Direction Nationale de la Recherche Scientifique et Technologique; Centre de Gestion de l'Environnement du Nimba-Simandou; Projet des Nations Unies de Développement; Comités Villageois de Surveillance; Ministère du Développement Durable et de l'Environnement, Direction Nationale des Forêts et Faune; Société des Mines de Fer de Guinée; Liberia - Forestry Development Authority, Office of the DMD/Forest Conservation; Arcelor-Mittal; Sierra Leone - Ministry Agriculture, Forestry and Food Security, Forests Conservation and Wildlife Unit, Wildlife Conservation Forestry Division.

The "Bundesamt für Naturschutz", Bonn issued CITES import permits (*Nimbaphrynoides o. occidentalis*; E-3117/07 and E-4074/08; *Nimbaphrynoides o. liberiensis*; E-4509/07), the "Le Directeur Nationale de la Protection de la Nature" (2007/00314) and "L'organe de Gestion CITES Guinée" (2008/0049) in Guinea (*Nimbaphrynoides o. occidentalis*) and the "Forestry Development Authority" in Liberia (01, *Nimbaphrynoides o. liberiensis*) the respective CITES export permits.

Sampling techniques Anurans were detected via visual, acoustic or opportunistic searches during the rainy seasons 1993, 1995, 2001 to 2005 and 2009 to 2011. Terrestrial and arboreal species were captured by hand and aquatic species, notably from the family Pipidae, by net. Digging was performed to sample fossorial species such as caecilians. Overall we screened 793 amphibians from 62 species (see app. 3.3-1 & 3.3-2) which originated from 64 sites throughout the region (tab. 3.3.1-1) as well as live individuals destined for export at Accra airport, Ghana (figs. 3.3.1-1, 3.3.1-2a & 3.3.1-b).

We used two methods: (i) epithelial swabbing and (ii) histology of phalanges to sample for *Bd* (Burrowes *et al.* 2011; Skerratt *et al.* 2011). Cotton swabs were utilised to brush the *Bd* sensitive areas of each individual live frog including the ventral surface of each thigh, hind foot and pelvis. Swabs were either placed in 95% ethanol or sprayed with ethanol and stored dry or stored dry directly and kept away from heat (Van Sluys *et al.* 2008). Toe clips were obtained from preserved adult frogs. A piece of dorsal skin was cut one third from the anterior tip of the body and stored in ethanol from preserved caecilians. Toe and skin samples were fixed and stored in 95% ethanol. The samples were analysed at the Museum für Naturkunde, Berlin (MfN; 78 swabs), the North-West University, Potchefstroom (NWU; 105 swabs; 137 toe tips for histology), the University of Washington (UW; 103 swabs) and the Institute of Zoology, London (IoZ; 372 swabs).

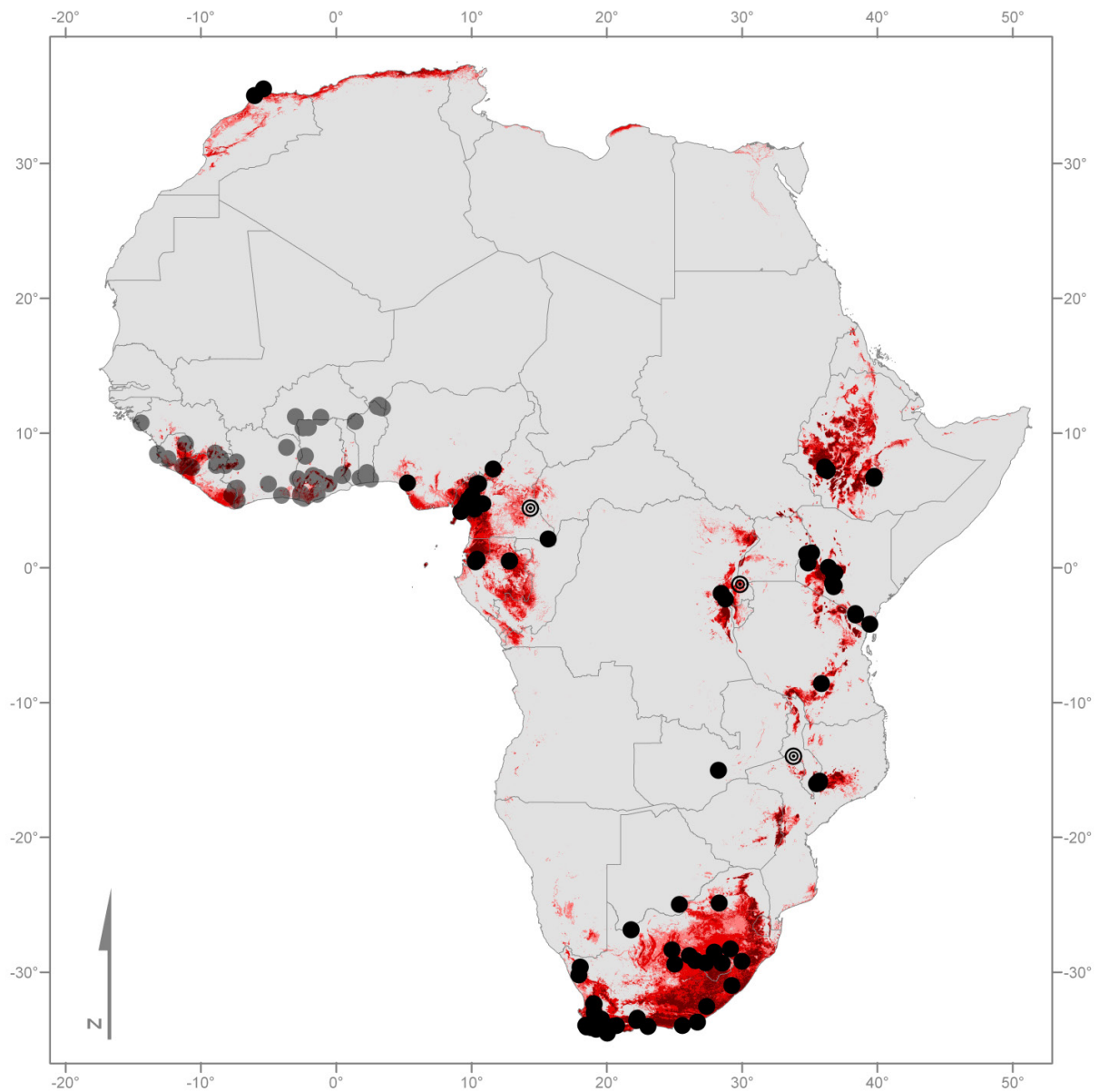


Fig. 3.3.1-1: Map of confirmed records of *Bd* on the African continent (black dots). Grey transparent dots represent the West African localities with negative *Bd* records. The hollow black circles indicate *Bd* positive localities (Soto-Azat *et al.* 2010) which were not used for modelling. The three red colours represent the geographical extent of three different models, predicting the potential distribution of *Bd*. Modelling is based on the conditions of sites with confirmed presence of the pathogen (light red = maximum; red = mean; dark red = minimum; for niche parameters see tab.3.3.1-2).



Voucher specimens and preserved individuals were euthanized (using either MS-222 or chlorobutanol), preserved in 75% ethanol and are deposited at MfN (134 specimens) or the Burke Museum of Natural History and Culture at UW (103 specimens).

3.3.1.3.2 Laboratory techniques

DNA was extracted with DNeasy extraction kits (Qiagen) following manufacturers protocol. DNA extractions were stored at -80°C (MfN, NWU, IoZ) or 4°C (UW) prior to analysis. At all laboratories, standards of known zoospore concentrations (100, 10, 1 and 0.1 zoospore genomic equivalents (IoZ, NWU, UW)) or ITS copies (169 copies per zoospore (MfN)) and a negative control were used in each diagnostic assay.

At MfN, NWU and IoZ, DNA was analysed using *Bd*-specific primers (ITS-1/5.8-S) and following the RT-qPCR protocol of Boyle *et al.* (2004). At IoZ, bovine serum albumin (BSA) was included in the Taqman mastermix to minimise inhibition of the PCR (Garland *et al.* 2011). The PCR profile was: 5 min at 96°C followed by 50 cycles of 10 s at 96°C and 1 min at 60°C. At all laboratories, a positive result consisted of a clearly sigmoid curve in duplicate samples. At UW, DNA was analysed by conventional PCR (Annis *et al.* 2004) and visualised on a 1.5% agarose gel. To verify that DNA extractions were successful, frog 16 s rRNA (16S) was amplified for each sample using standard amphibian primers (Vences *et al.* 2005). As an additional positive control, the universal fungus primers ITS-4/ITS-5 (White *et al.* 1990) were used to amplify DNA from various (non-*Bd*) chytrid genera that were extracted from epithelial swabs. The presence/absence of *Bd* was tested by using the *Bd*-specific primers Bd1a/Bd2a (Annis *et al.* 2004).

Toe clips were dehydrated in an alcohol series (70%, 96% and 2 x 100% alcohol), elucidated with xylene and infiltrated with paraffin wax at 60°C. Following the wax infiltration the tissues were embedded in paraffin wax blocks using a SLEE MPS/P2 embedding centre and sectioned at 6 mm with a Reickert-Jung 2050 automated microtome. Sections were stained with Mayer's haematoxylin and counter stained with eosin. Slides were then examined under a Nikon Eclipse E800 compound microscope for the presence of *Bd* using the criteria described in Berger *et al.* (1999, 2001).

Tab. 3.3.1-1: Number of amphibian samples per West African country tested for the presence of *Bd*. Swab = molecular investigation of swab sample; toe/skin = histological examination of toe tips (anurans) and skin pieces (caecilians).

Country	Swab	Toe/Skin	Total
Bénin	120	13	133
Burkina Faso	0	3	3
Côte d'Ivoire	29	26	55
Ghana	254	36	290
Guinea	243	44	287
Liberia	10	4	14
Sierra Leone	0	11	11
Total	656	137	793

3.3.1.3.3 Environmental Niche Modelling

ENM is a statistical modelling tool where a priori set algorithm searches relationships within the data (as opposed to process based modelling). Our ENM relies on maximum entropy principles (using the software Maxent 3.3.3.k (Phillips *et al.* 2004, 2006; Phillips & Dudík 2008). The approach basically compares the values of the variables at the sites where a species is present against a background sampled from sites with no presences. Maxent uses machine learning to maximise the entropy function; but see Elith *et al.* (2011) for a detailed description of

the statistics. Despite the number of available algorithms, Maxent is one of the best ENM techniques when using presence-only data (e.g. Elith *et al.* 2006; Heikkinen *et al.* 2011).

Herein we report absence of *Bd*. Nevertheless, the true absence of organisms is in general difficult to ascertain (e.g. compare the findings from Daversa *et al.* (2011) and Bell *et al.* (2011)). Therefore we applied the most conservative method using only confirmed presences from the African continent with a high spatial certainty for our ENMs ($n = 112$ reported records; see app. 3.3-3). The aim was to model the likely geographic distribution of *Bd* and strictly avoid type II errors.

We used 17 environmental parameters on a 30 arc second grid (which equals roughly 1 km²) for the whole African continent as variables in our ENM. All parameters were continuous (not categorical) and are classified into three broad categories: climate, environment and altitude. The climate variables comprised ten parameters, all averaged from 1950 to 2000. Five environmental parameters were obtained from two satellite imagery data sets with different spectral sensitivities (SPOT4 & MODIS). Altitude was converted into two parameters calculated from a radar derived data set (SRTM) (see tab 3.3.1-2).

Tab. 3.3.1-2: Environmental parameters used in the environmental niche modelling (ENM) approach with a short description of the parameter and the source of the original data. Parameters 1–10, calculated in two steps: i) an average (from the years 1950 to 2000) for each month (January to February), thus leading to 12 averages; (ii) calculation as detailed in the main text. Parameters 11–12: calculated from the annual average of the year 2000. Parameters 13–15: extracted from the 500 m MODIS vegetation continuous fields dataset, which are derived from monthly composites that are in turn derived from eight day composites. All 7 bands were used and smoothed via a 4x4 rectangular neighbourhood function. Parameters 16–17: after calculation data were ln-transformed and multiplied by 10 to assure compatibility with other environmental parameters.

No.	Category	Parameter	Description	Original source
1	climate	tmax_low	lowest value of the maximum temperatures	Hijmans <i>et al.</i> 2005
2	climate	tmax_high	highest value of the maximum temperatures	Hijmans <i>et al.</i> 2005
3	climate	tmax_std	standard deviation the maximum temperatures	Hijmans <i>et al.</i> 2005
4	climate	tmin_low	lowest value of the minimum temperatures	Hijmans <i>et al.</i> 2005
5	climate	tmin_high	highest value of the minimum temperatures	Hijmans <i>et al.</i> 2005
6	climate	tmin_std	standard deviation of the minimum temperatures	Hijmans <i>et al.</i> 2005
7	climate	prec_high	highest precipitation value (wettest month)	Hijmans <i>et al.</i> 2005
8	climate	prec_low	lowest precipitation value (driest month)	Hijmans <i>et al.</i> 2005
9	climate	prec_std	standard deviation of the precipitation	Hijmans <i>et al.</i> 2005
10	climate	prec_sum	total annual precipitation	Hijmans <i>et al.</i> 2005
11	environment	glc2	vegetation derived from the near-infrared (0.78–0.89 μ m) wavelength of the SPOT4 satellite	Arnaud & Leroy 1991
12	environment	glc3	vegetation derived from the red (0.61–0.68 μ m) wavelength of the SPOT4 satellite	Arnaud & Leroy 1991
13	environment	bare	percentage of bare ground (MODIS)	Hansen <i>et al.</i> 2003a
14	environment	herb	percentage of herbaceous ground cover (MODIS)	Hansen <i>et al.</i> 2003b
15	environment	tree	percentage of woody vegetation (MODIS)	Hansen <i>et al.</i> 2003c
16	altitude	srtm_c	elevational contrast calculated from the SRTM30 dataset using a 3x3 moving window	Farr <i>et al.</i> 2007
17	altitude	srtm_v	elevational variance calculated from the SRTM30 dataset using a 9x9 moving window	Farr <i>et al.</i> 2007

In total we calculated 100 ENMs. Models were replicated using sub sampling. For each model, points were randomly allocated into two groups: 70% ($n = 79$) for model training and 30% ($n = 33$) for model testing. From these 100 models three average models were derived: maximum, mean and minimum predictions gained. The maximum, mean and minimum models used the average 10 percentile thresholds over all 100 models to gain three binomial models. Models were validated via the area under the curve (AUC) criterion, which refers to the receiver operating characteristic (ROC) curve. This measurement is threshold-independent and commonly used for such models (e.g. Elith *et al.* 2006).

3.3.1.4 Results and Discussion

Despite our extensive sampling on a species and geographical level, we did not detect any evidence of *Bd* in the investigated sites, neither by molecular (at least, any strain known to cause severe chytridiomycosis (Farrer *et al.* 2011)) nor by histological investigations. Hence, the only region in sub-Saharan Africa without any confirmed records remains the Upper Guinea Forests and the surrounding savannahs.

One positive *Bd* record from Ghana (Parker *et al.* 2002) is often cited in the literature and has been used for ENMs (Ron 2005; Rödder *et al.* 2008; Puschendorf *et al.* 2009). However, it was excluded from our ENM analysis because the specimen stems from the pet trade, has an unknown origin and was tested after being imported into the US. Thus, the specimen could have contracted the pathogen from anyone of a number of possible sources within the trade pathway. Further support for our decision stems from finding that infections at the population level are highly dependent on the density of individuals (Briggs *et al.* 2010; Stockwell *et al.* 2010). Crammed conditions are common in the pet trade and prevalence is high in traded amphibians (Schloegel *et al.* 2009, 2010; Catenazzi *et al.* 2010; Bai *et al.* 2012). In addition, no other *Bd* record was reported from Ghana ($n = 292$, this paper).

3.3.1.4.1 Continental Modelling

In contrast to these findings our ENMs show that *Bd* could potentially occur in West Africa. So far *Bd* has never been recorded west of Okomu National Park, which lies east of Lagos, Nigeria (see figs. 3.3.1-1 & 3.3.1-2b). As the fungus prefers moist and comparatively cooler environments (Berger *et al.* 2004; Piotrowski *et al.* 2004; Drew *et al.* 2006; Bosch *et al.* 2007; Kriger & Hero 2007a, 2007b; Longcore *et al.* 2007; Murray *et al.* 2009; Skerratt *et al.* 2010), we hypothesise that the Dahomey Gap, a naturally non-forested stretch ranging from eastern Ghana to western Nigeria, consists of unsuitable habitats and therefore provides a distributional barrier (fig. 3.3.1-2c). However, this hypothesis must be treated cautiously because *Bd* can survive outside its preferred temperature range (Piotrowski *et al.* 2004; Woodhams *et al.* 2008) and could therefore cross the Dahomey Gap. In addition a number of other factors may influence its persistence as well (e.g. life-history stage at exposure (Lamirande & Nichols 2002; Carey *et al.* 2006), host immunity (Ribas *et al.* 2009), host stress levels Burgin *et al.* 2005) and anthropogenic influences (St.-Amour *et al.* 2008; Becker & Zamudio 2011)).

Overall the ENMs performed well, with a mean training AUC of 0.979 ± 0.002 and testing AUC = 0.9676 ± 0.010 . All 17 selected variables contributed to the models. The highest contribution came from the “minimum precipitation” (prec_low 35.3%), followed by the “variance in elevation” (srtm_v 22.6%) and the “lowest value of the maximum temperatures” (tmax_low 17.5%). Jackknife testing revealed “highest value of the maximum temperatures” (tmax_high) as the variable with the greatest information content when used alone (for details see app. 3.3-4). Until now no fine-grained continental ENM existed, only coarser ones (2.5 arc minutes) on a global scale (see Puschendorf *et al.* 2009; Murray *et al.* 2011). Our models showed that *Bd* could occur in the investigated region but not as widespread as in some other parts of Africa. Only a few West African areas were predicted as suitable for *Bd*. These are primarily the comparatively wetter or higher altitude areas of the Upper Guinea forests (see fig. 3.3.1-2a). Our modelling results show a picture different to the recent global modelling approaches for *Bd* (Ron 2005; Rödder *et al.* 2009). The main differences are that large areas in Angola, Namibia and Zambia predicted by Ron (2005) and Rödder *et al.* (2009) are not predicted in our approach. Other differences concern areas in western Africa where our ENM predict a smaller range compared to Ron (2005) and Rödder *et al.* (2009). Interestingly large areas in Ethiopia are predicted to be highly suitable for *Bd* by all approaches. Similarly, a narrow region in northern Africa, ranging from Tunisia over Algeria to Morocco was predicted. ENMs for both regions were recently confirmed by respective positive *Bd* records (El Mouden *et al.* 2011; Gower *et al.* 2012). The causes for the differences between our ENMs and previous ones are complex. The models differ substantially in the parameter setting of the algorithm, their resolution, the points used, and the environmental parameters.

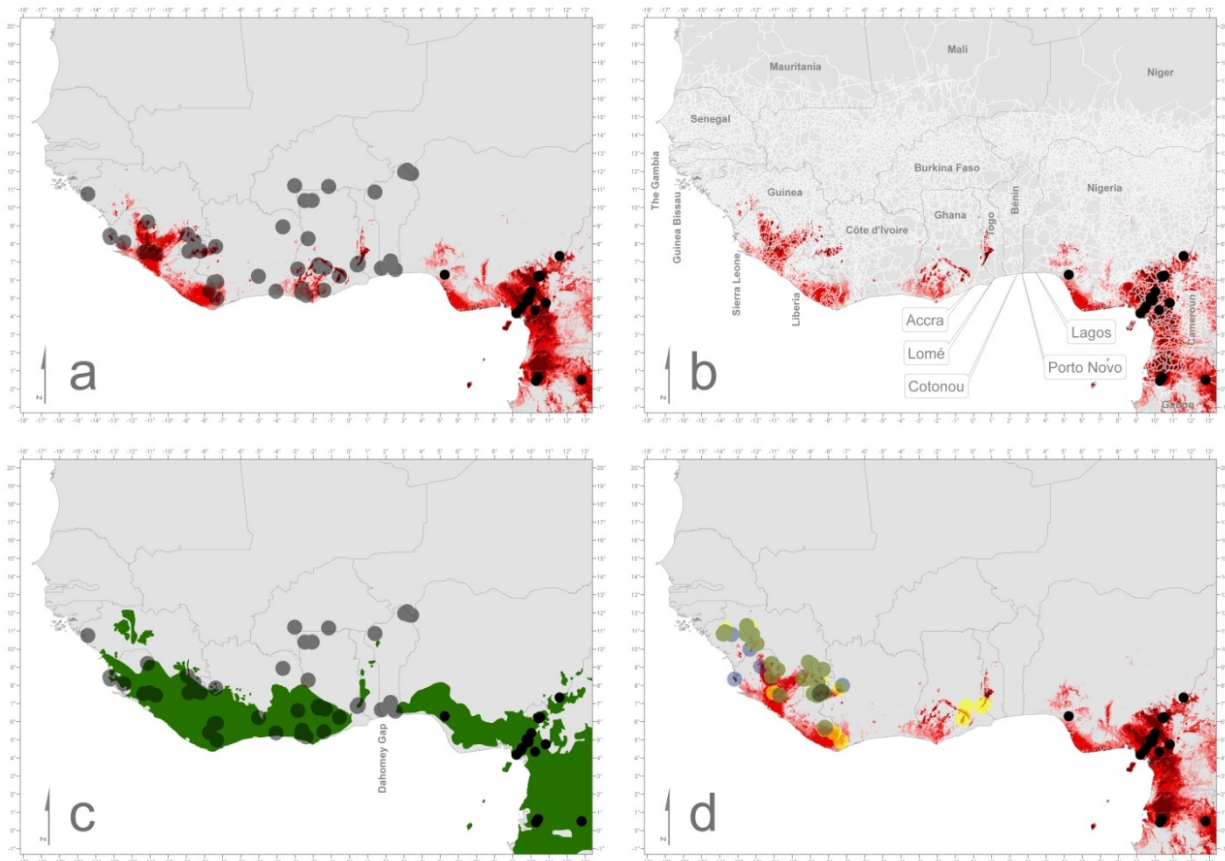


Fig. 3.3.1-2: Detailed maps of West Africa. From top to bottom, depicting the most western positive records of *Bd* (black) and the negative records (transparent grey) (2a). Fig. 2b indicates in white transparent lines the transport system (roads) of the region. If *Bd* is transported via humans, the area around Accra (Ghana) is most likely to be the point of introduction (well connected via transportation routes and highly suitable environment). Further shown (2c) are the extents of the potentially forest regions (green) with the Upper Guinea Forests west of the Dahomey Gap [after 131,2a]. In 2d the known point localities of *Conraua alleni* (transparent yellow), *Petropedetes natator* (transparent blue) (light green = overlapping localities), and *Nimbaphrynoides occidentalis* (dark green) are depicted.

The origin of *Bd* is still unknown. One hypothesis was that the pathogen originated in Africa and spread globally via the commercial trade of clawed frogs (Pipidae: *Xenopus* spp.). Histological and molecular analyses (Weldon *et al.* 2004; Soto-Azat *et al.* 2010), detailed trade history (Weldon *et al.* 2007) and known occurrences at that time (Hopkins & Channing 2003; Goldberg *et al.* 2007; Greenbaum *et al.* 2008) supported this hypothesis (see also Bell *et al.* 2011; Kielgast *et al.* 2010). In addition the oldest known record originated from Cameroon, more specifically *Bd* was detected in a museum voucher of *Xenopus fraseri*, collected in 1933 from lowland rainforest (Soto-Azat *et al.* 2010). Now an older record from Japan, dated to 1902 (Goka *et al.* 2009), challenges the hypothesis that *Bd* originated in Africa. However, there is more than one lineage of *Bd* (Goka *et al.* 2009; Farrer *et al.* 2011; Schloegel *et al.* 2012) and one or more pathogenic lineages could have spread out of Africa.

This leads to the question of how *Bd* is transported from one location to another. Trade of live animals is commonly suggested as the most likely means of dispersal (Waldmann *et al.* 2001; Mazzoni *et al.* 2003; Weldon *et al.* 2004; Garner *et al.* 2006; Fisher & Garner 2007; Skerratt *et al.* 2007; Schloegel *et al.* 2009, 2010, 2012; Kriger & Hero 2009; Farrer *et al.* 2011; Weldon & Fisher 2011). However, recent findings support the notion that other dispersal vectors are also possible such as reptiles, birds or mammals (Johnson & Speare 2005; Kilburn *et al.* 2011; Garmyn *et al.* 2012).



3.3.1.4.2 Potential Error Sources

We herein did not find any evidence for *Bd* in West Africa. Several explanations are plausible why *Bd* was not recorded in our study area. Either (i) sampling was flawed if *Bd* follows seasonal patterns and we sampled during a low prevalence cycle (e.g. Kriger & Hero 2007a; Whitfield *et al.* 2012) or (ii) species were sampled whose ecological niches do not or only slightly overlap with that of *Bd* (e.g. Kriger & Hero 2007b; Woodhams *et al.* 2007; Murray *et al.* 2012). Other possibilities are (iii) that sampling in the field failed, e.g. due to blemished preservation (e.g. Van Slyus *et al.* 2008; Soto-Azat *et al.* 2009) or (iv) poor diagnostic assays, e.g. presence of PCR inhibitors (e.g. Hyatt *et al.* 2007). Although possible, it is unlikely that *Bd* was not detected due to aforementioned errors. Seasonality might be a problem. We sampled mainly during the wet season and even in highly seasonal *Bd* infected regions, positive confirmation is possible year round (Kinney *et al.* 2011) though not everywhere (Berger *et al.* 2004; Kriger & Hero 2007b; Conradie *et al.* 2011; Whitfield *et al.* 2012).

We sampled species with ecological requirements strongly overlapping with the fungus, including avoiding xeric species such as *Amietophrynus xeros* or *Tomopterna cryptotis*. Many of the sampled genera have previously been shown to be infected with *Bd* in other African regions (e.g.: *Amietophrynus* (mean prevalence 21.05%; Bayesian credible interval 11.13–36.46%), *Hyperolius* (39.51%; 35.26–43.92), *Leptopelis* (28.57%; 22.03–36.18%), *Petropedetes* (11.11%; 15.17–65.11%), *Phrynobatrachus* (17.65%; 9.63–30.32%), *Ptychadena* (26.26%; 20.36–33.17%), *Xenopus* (3.35%; 2.35–4.77%) (calculated from Weldon *et al.* 2004; Goldberg *et al.* 2007; Greenbaum *et al.* 2008; Kielgast *et al.* 2010; Bell *et al.* 2011; Reeder *et al.* 2011; Balázš *et al.* 2012; Gower *et al.* 2012; Doherty-Bone *et al.* 2013)).

Thirdly, anuran tissue samples, from which DNA was successfully extracted, were preserved following the same procedures as *Bd*-swabs and toe clips. In addition all methods used in this paper have already detected *Bd* in samples from other regions (see method section and Weldon *et al.* 2004; Doherty-Bone *et al.* 2013).

Lastly, amplification of DNA from frog 16 s and fungal ITS regions for the samples at UW (n = 103) demonstrate that swabbing was effective (see app. 3.3-2). In terms of numbers of individuals and geographical scale, our sample size is also large enough to make a confident diagnosis. All the above mentioned facts support our conclusion that our sampling is representative for West African amphibians and that *Bd* is highly likely to be absent in western Africa.

3.3.1.4.3 Conservation implications

Though *Bd* has been detected in a number of species with different ecological niches, most populations which are adversely affected by the fungus are from higher altitudes and inhabit mostly flowing streams (see above and Bancroft *et al.* 2011; Murray *et al.* 2012). Therefore three West African species are of major conservation concern with regards to *Bd* infection: *Nimbaphrynoides occidentalis* (samples tested herein: n = 62), *Conraua alleni* (n = 86) and *Petropedetes natator* (n = 158). The Nimba toad, *N. occidentalis*, is the only truly viviparous anuran species and is restricted to narrow ranges of high altitude grasslands of the Nimba Mountains, which are situated at the border between Guinea, Liberia and Côte d'Ivoire (Hillers *et al.* 2008d; Sandberger *et al.* 2010 and citations therein). This species is listed as “Critically Endangered” because of its very small distribution range and the decline of suitable habitats (IUCN 2011). *C. alleni* and *P. natator* are frogs occurring in streams, mostly in mountainous forest habitats. They are listed as “Vulnerable” and “Near Threatened” respectively (IUCN 2011).

The geographic distributions of all three species show a high overlap with the potential geographic ENM distribution of *Bd*. The models highly predict the occurrence of *Bd* in areas where all three species can be found (fig. 3.3.1-2d). The fact that *N. occidentalis* is independent of flowing streams does not necessarily render this species less susceptible to *Bd*, as *Bd* has already been detected in at least three African species without aquatic larval stages: *Nectophrynoides asperginis* (Weldon & du Preez 2004; Channing *et al.* 2006) (though note that



the species lived (extinct in the wild) in the spray zone of Kihansi River Gorge, Tanzania), *Arthroleptis* sp. (in Gabon (Bell *et al.* 2011) and in Malawi (Conradie *et al.* 2011)) and the suspected direct developer *Balebreviceps hillmani* (in Ethiopia (Gower *et al.* 2012)). *Bd* is also suspected to be responsible for the extinction of four other direct developing species (= no aquatic larval stage): *Craugastor milesi* (from Honduras), *Rheobatrachus silus*, *R. vitellinus*, and *Taudactylus diurnus* (from Australia). Though heavy logging occurred in the areas of distribution of the Australian species as well and all four species are associated with water (*C. milesi* adults live along rivers; *R. silus* & *R. vitellinus* have aquatic adults; *T. diurnus* lays eggs in water) (Stuart *et al.* 2008; IUCN 2011). Therefore, we conclude that *Bd* could potentially occur in western Africa due to the availability of suitable habitats and susceptible hosts.

Our sampling covers a representative subsample of West African species. This is not only due to the number of species sampled but also due to the fact that two species have been intensively sampled, which are habitat generalists (app. 3.3-1) and have a wide distribution, i.e. *Phrynobatrachus latifrons* (n = 79) and *Hoplobatrachus occipitalis* (n = 67) (Rödel 2000). The latter species is also the major traded species in local and regional food markets and is therefore transported over long distances (Mohneke *et al.* 2010). The species is also transported across the Dahomey Gap, more specifically from north-eastern Bénin to south-western Nigeria and probably even further eastwards (Mohneke *et al.* 2009; Mohneke *et al.* 2010). Thus the possibility that *Bd* will be spread from Nigeria to the west is reduced.

We will briefly highlight the most likely entry points for *Bd* from Central Africa to West Africa. Looking at the major transportation routes, a human *Bd* transport distribution will in all likelihood first be detected in the region around Accra (fig. 3.3.1-2b). A highway exists parallel to the coast and connects the major cities (Lagos, Nigeria; Porto Novo & Cotonou in Bénin, Lomé, Togo; Accra, Ghana). Environmental suitability for *Bd* is low in Bénin and Togo, making Ghana a more likely entry point for *Bd*. Railways exist but mainly in north-south directions and rarely cross international borders. They operate also on a rare and infrequent basis and are not a major means of transportation. The introduction of *Bd* into West Africa via animate vectors is much more difficult to predict. The most likely entry point for them would be either the highlands of Togo or the Atewa range in Ghana (fig. 3.3.1-2b), because they are closest to the *Bd* positive localities in Nigeria (Okomu NP) and are environmentally suitable for *Bd*.

Every effort has to be made to ensure that *Bd* will not invade western Africa, especially because threats are additive (e.g. Wake 2012) and fragmentation has already affected the region heavily (see Chatelain *et al.* 1996, 2004; Mayaux *et al.* 2004). The situation is similar to Madagascar where *Bd* has also not been detected (Weldon *et al.* 2004, 2008; Vredenburg *et al.* 2012). For environmental work in the region (e.g. consultant, scientific) we strongly recommend buying new equipment. This has to include the disinfection of materials and equipment transported from *Bd* positive to *Bd* negative regions, especially to *Bd* sensitive regions for example by mining companies as these sensitive areas often coincide with proposed mining areas (see Johnson *et al.* 2003; Webb *et al.* 2007; Schmidt *et al.* 2009; Phillott *et al.* 2010; Murray *et al.* 2011). The same precautionary measures should apply for the ecotourism industry (see Wollenberg *et al.* 2010). Only through acute scientific observation, greater collaboration between conservation and all sectors of industry and commerce can some measure of control be achieved over the spread of wildlife pathogens such as *Bd*.





3.4 Niches of West African amphibians

The following chapter is divided into two parts. In the first part, alpha diversity of amphibians in West Africa is assessed. The second part incorporates additional information on niches of West African amphibians and provides a simple answer to the question why species ranges differ

3.4.1 Leaping forward - Providing the spatial baseline for amphibian conservation across West Africa

3.4.1.1 In a nutshell



Conservation needs fine scaled distribution data covering large geographic spaces to take informed decisions on questions such as which areas do need protection and where to set priorities. However, most data are available as occurrence records which results in patchy maps. In addition, not all regions are equally well sampled and Africa remains comparatively under-sampled for most taxa. We extrapolated species distributions from point records (total of 15,944 records on a 30arc seconds grid for 176 amphibian species) species into a large geographical region, using Environmental Niche Modelling as a tool and employing 18 environmental parameters.

This provides for the first time a fine scale distribution map of amphibian alpha diversity for the entire West African region. Already known centres of high diversity were confirmed (e.g. south-western Ghana and south-eastern Côte d'Ivoire) and potential new ones suggested (e.g. northern Liberia and borders with Guinea and Sierra Leone). The areas of high diversity were only partly in accordance with global identifications of priorities such as the hotspot by Conservation International and the ecoregion analyses by the World Wide Fund for Nature. This further highlights the importance of fine scaled approaches. The areas of amphibian diversity were also only partly covered by the existing protected area network. Furthermore, subsets of the entire amphibian fauna (threatened, endemic and evolutionary distinct species) were analysed, which provided more in depth details of the areas which are important for amphibian conservation. In addition, we imply that from a methodological point of view, it is highly important to utilise spatial filters to correct spatial models for biogeographical barriers.

3.4.1.2 Introduction

Conservation planning needs to know how biodiversity is distributed, because efforts have to be focused and prioritised (e.g. Pimm *et al.* 1995; Bottrill *et al.* 2008). Therefore decision makers in the conservation realm might for example ask which places harbour a high diversity or which places contain many unique or threatened taxa (see review by Brooks *et al.* 2006). This already implies that organisms are not uniformly distributed. A common and straight forward way to visualise these differences, e.g. in diversity, is overlaying species occurrences and then identifying areas of high species richness. Immediately, many practical problems arise from such an approach. Two major ones are: (i) how is occurrence measured, e.g. which type of extrapolation should be used (e.g. expert opinion, simple polygons, kernels, habitat suitability maps) and (ii) how the overlay process is done (i.e. which diversity index to choose). In the following we will highlight practical issues from a conservation point of view and provide possible solutions.

First, what is a “good” measure of occurrence? It is impossible to precisely map the range of a species over its whole range and over all scales (see Pearson & Dawson 2003). Besides the problems of detection probabilities (e.g. Gibson 2011; Wintle *et al.* 2012), the amount of resources needed (e.g. man power, budget), quickly become larger than the net gain. Furthermore, changes in scale require changes of environmental factors which can be used to explain as well as to extrapolate species distributions, e.g. soil types being responsible on local; but climate on a global scale (Pearson & Dawson 2003). Compared to temperate regions, data availability in the tropics is usually even worse due to higher species richness, higher proportion



of rare species and usually fewer studies. The amount of studies differs also substantially between different tropical regions, whereupon Africa remains something like the global “dark spot” (Collen *et al.* 2008). So, aside all these problems, how is presence data usually presented? Existing data almost exclusively come as point localities with very variable spatial coverage, though often these are extrapolated via expert opinion, resulting in planar occurrences and richness maps (e.g. see IUCN 2013).

Second, the question arises how diversity should be measured. The measurement of choice should allow comparisons between different areas or studies and follow certain statistical requirements (see Jost 2007 for details). It is commonly acknowledged that species diversity can be partitioned in two components: richness and evenness. Richness is the total number of species and evenness takes their relative abundance into account. To clarify the concept, three types of diversity are named, depending on the question asked: alpha, beta and gamma diversity (see Whittaker 1960, 1972 for the original concept). Alpha diversity is the diversity of a single site, community or assemblage (e.g. Magurran & McGill 2011). The precise concept of beta diversity is still subject to debate but in our context can be broadly termed as changes (e.g. species turnover) between different sites, communities or assemblages (see reviews by Tuomisto 2010a, b, c). Finally, gamma diversity is measured across a landscape or ecosystems and defined as product of alpha and beta (see Jost 2007; Tuomisto 2010c) thus measuring diversity on a much larger scale. A number of diversity indices exist; their usage depending on the concept used and the question asked. Recent publications have clarified what the statistical properties of such indices should be (e.g. multiplicative partitioning) and proposed algorithms to calculate them (Jost 2007, 2010; Baselga 2010, 2012; Chao *et al.* 2012; Tuomisto 2012).

The above mentioned diversity measures either treat all species equally (pure richness) or weigh them according to their relative abundance (when evenness is included). However, other measures, commonly used to grasp and match the complexity of species distributions is how unique taxa are. Taxa can be unique due to their threat status (e.g. Red List), unique to a specific area (endemic) or unique in phylogenetic/evolutionary terms (evolutionary distinct). The “evolutionary distinctness” concept was developed by the “Edge of existence programme” and ranked known amphibian and mammal species according to their evolutionary uniqueness, also combining that measure with their threat status (Isaac *et al.* 2007, 2012; Collen *et al.* 2011). The combination of a high number of endemic and threatened species was used to identify a set of global hotspots (Myers 1988, 1990; Myers *et al.* 2000; Mittermeier *et al.* 2004). One of these hotspots is the “Guinean forests of West Africa”. Recently, it was shown that for amphibians, which are up to date the most threatened vertebrate group on earth (IUCN 2013), this hotspot actually comprises two distinct biogeographic regions: a “true” West African and a Central African region, the latter actually comprising the Cameroon highlands. Amphibian assemblages from both regions have only few species in common (Penner *et al.* 2011). The latter analyses also showed that further subunits exist within the West African region. However, this study did not allow for biogeographic conclusions on small scale as spatial coverage was too coarse for parts of the covered region. Nevertheless, conservationists need detailed (fine grained) distribution data to inform decision processes.

Herewith, we use West African amphibians as a model for such an approach. We use point occurrence data and statistical modelling to extrapolate from the single occurrences and to gain a complete coverage of the West African region with a high spatial resolution. We address the following questions: How is the amphibian diversity distributed within West Africa? More specifically where are centres of special conservation interest in terms of an overall high diversity and uniqueness. Thus how are threatened, endemic and evolutionary distinct amphibian species distributed? In other words, where are hotspots within a hotspot? Furthermore, we compare our findings to existing protected areas and point out areas where urgent efforts are needed to prevent loss of amphibian diversity. Finally from an analytical point of view we assess the importance of two methodological aspects (spatial filtering and choice of diversity measure).



3.4.1.3 Material & Methods

3.4.1.3.1 Amphibian data

3.4.1.3.1.1 Definition of included taxa

Previous work showed that West Africa has unique amphibian assemblages (Penner *et al.* 2011). Therefore the geographic region of West Africa, from an amphibian point of view, is well defined. In the north the Saharan desert provides a natural delineation between North Africa and sub-Saharan Africa (e.g. Poynton 1999). The major geographic division towards Central Africa is the Cross river in south-easternmost Nigeria. For simplicity we herein used the border between Nigeria and Cameroon (see Penner *et al.* 2011). Thus, all amphibian species occurring south of the Saharan desert and inside all countries west of Cameroon, were included in the present work. This resulted in a total of 181 taxonomically known species. Three species were deleted from the list due to doubtful taxonomic status in West Africa (*Arthroleptis variabilis*, *Leptopelis bequaerti* & *Hyperolius adspersus*). However, several species are known to consist of species complexes. Their taxonomic treatment is work in progress (Rödel, Barej and co-workers). Therefore a total of 192 taxonomic units, corresponding to valid species and confirmed candidate species (*sensu* Vieites *et al.* 2009) were recognised. We were able to calculate statistical models for 176 taxa. The missing 16 taxa did not have sufficient occurrence records (see results). Taxonomy applied follows Frost (2013).

3.4.1.3.1.2 Identification of unique amphibians

To identify unique amphibians we classified the taxa according to their threat status (i), endemism (ii), and evolutionary distinctness (iii). i) Information on the threat status of each taxon was taken from the IUCN Red List (IUCN 2013). For taxa not assessed yet, a tentative category was assigned; strictly following the Red List Assessment guidelines (see IUCN 2013) and taking a conservative approach meaning that new categorical assignments are based on closely related species which have already been assessed. In cases where we have accepted candidate species for our analyses, the candidate species resulted from a split of the original taxon. Thus a formal assessment will probably lead to even higher threat classifications, mainly due to overall smaller distribution ranges of every particular candidate species. ii) Endemism in our case was defined as either being endemic to West Africa (all taxa occurring only West of Cameroon) or endemic to the Upper Guinea forests (all taxa occurring only within the ecoregions Western and Eastern Upper Guinea forests; see Burgess *et al.* 2004). iii) The ten most evolutionary distinct species were identified by ranking species according to the “evolutionary distinct” (ED) score values for taxa recognised by Isaac *et al.* (2012). The combination of the threat status (i) and the ED score (iii) resulted in the score “evolutionary distinct and globally endangered” (EDGE).

3.4.1.3.2 Environmental niche modelling

Distribution maps may be created applying different approaches. Alternative to expert opinion, statistical modelling techniques can be used to extrapolate from point occurrences into a planar space. In general, this requires presences and absences. However, for our data set, absences are impossible to ascertain. So, methods have to be used which create artificial absences and compare these against environmental variables, thus modelling the Grinnellian niche measured by scenopoetic variables (Peterson *et al.* 2011). We used such an environmental niche modelling (ENM) technique relying on maximum entropy principles (Maxent; Philips *et al.* 2004, 2006; Philips & Dudík 2008). The algorithm employs machine learning methods to compare niche parameters derived from presences (occurrence records) against niche parameters from background data (artificial absences) by “minimising the relative entropy between the two probability densities” (Elith *et al.* (2011); see that paper also for a detailed description of the underlying statistics). Maxent is commonly evaluated as one of the best ENM techniques when using presence-only data (e.g. Elith *et al.* 2006, Ortega-Huerta & Peterson 2008; Heikkinen *et al.* 2011). Point distribution records were collected from own surveys, surveys of colleagues, the



literature and two databases (GBIF 2013 and HerpNet 2013). All records were checked for plausibility and overall 15,944 point occurrences were finally used for the modelling approaches.

In our models we used 18 variables as environmental parameters reflecting climate, vegetation, altitude and distance to river (see tab. 3.4.1-1; refer to Gschweng *et al.* 2012; Penner *et al.* 2012 for detailed descriptions). All variables are continuous and discretized on a 30 arc second grid (roughly 1km²). Models were run with standard settings, apart from the number of maximum iterations, set to 10,000, and the regularisation multiplier, set at 2.5 to reduce over-fitting (see Gschweng *et al.* 2012). Model validation was done via the area under the curve (AUC) criterion, which relates to the receiver operating characteristic (ROC) curve. This measurement is regarded as threshold-independent and a common measure for ENMs (e.g. Elith *et al.* 2006).

Tab. 3.4.1-1: Environmental parameters used in our ENMs. For details see Penner *et al.* 2013 (no. 1-17) and Gschweng *et al.* 2012 (no. 18) for descriptions of the parameters and their original sources.

No.	Category	Parameter	Description
1	climate	tmax_low	lowest value of the maximum temperatures
2	climate	tmax_high	highest value of the maximum temperatures
3	climate	tmax_std	standard deviation the maximum temperatures
4	climate	tmin_low	lowest value of the minimum temperatures
5	climate	tmin_high	highest value of the minimum temperatures
6	climate	tmin_std	standard deviation of the minimum temperatures
7	climate	prec_high	highest precipitation value (wettest month)
8	climate	prec_low	lowest precipitation value (driest month)
9	climate	prec_std	standard deviation of the precipitation
10	climate	prec_sum	total annual precipitation
11	environment	glc2	vegetation derived from the near-infrared (0.78-0.89µm) wavelength of the SPOT4 satellite
12	environment	glc3	vegetation derived from the red (0.61-0.68µm) wavelength of the SPOT4 satellite
13	environment	bare	percentage of bare ground (MODIS)
14	environment	herb	percentage of herbaceous ground cover (MODIS)
15	environment	tree	percentage of woody vegetation (MODIS)
16	altitude	srtm_c	elevational contrast calculated from the SRTM30 dataset using a 3x3 moving window
17	altitude	srtm_v	elevational variance calculated from the SRTM30 dataset using a 9x9 moving window
18	dist. to river	hydro	distance to nearest river

All ENMs were calculated for the entire African continent. Afterwards they were clipped back to the West African region for further analyses. The successful ENMs were cut at the “10 percentile training presence” (10p) threshold of each individual ENM, where 90% of the occurrences are correctly identified after cross-validation. Furthermore, the ENMs were also spatially filtered. Currently the algorithm and parameters do not take into account many factors which are known to shape species distribution, e.g. biotic factors such as competitive exclusion, dispersal limits, geographical barriers (see review by Wisz *et al.* 2013). Thus, if the “niche” is calculated it does not take into account e.g. whether a species is actually present in or close to the predicted area, if geographical barriers prevented its immigration or if another species already occupies that niche. Several techniques exist to correct that (Griffith 2003; De Marco *et al.* 2008; Blach-Overgaard *et al.* 2010). In our case all ENMs were spatially filtered via expert opinion. In the vast majority of taxa (n = 174) this was readily achieved because the ENM already depicted existing and known geographical barriers (compare to Penner *et al.* 2011) where models were cut. In the two remaining cases (the local endemics *Arthroleptis nimbaensis* & *Hyperolius nienokouensis*) a 50km buffer was set around the known occurrences to correct the ENM. Afterwards ENMs were converted into binary maps. For the following analyses, three data sets were created, each presenting a different step of the above mentioned workflow:

- a) untreated - non-linear likelihood ENMs for all species, no spatial filtering
- b) treated 1 - non-linear likelihood ENMs for all species, cut at 10p threshold and spatially filtered
- c) treated 2 - binary ENMs (presence & absence) for all species, cut at threshold and spatially filtered

3.4.1.3.3 Diversity measures

In order to analyse species diversity we calculated two different diversity indices for each grid cell. First, “true” alpha diversity $\alpha_{i,j}$ (after Jost 2007) was computed by

$$(1) \quad \alpha_{i,j} = \exp\left(-\sum_{k=1}^S p_k^{(i,j)} \ln(p_k^{(i,j)})\right)$$

taking into account the likelihood ENM $p_k^{(i,j)}$ for the k -th of S total species in the grid cell with row and column index i and j respectively. This index is suitable for the data sets a) and b).

Second, species richness $r_{i,j}$ for the data set c) was calculated by summing all binary presence values $q_k^{(i,j)}$, i.e.

$$(2) \quad r_{i,j} = \sum_{k=1}^S q_k^{(i,j)}.$$

3.4.1.3.4 Implementation

ENMs were calculated in Maxent (3.3.3.k, see above) and handled (mapping, richness, log transformations) in ArcGIS (version 10.0, Spatial Analyst extension, ESRI 2010). Statistics were calculated in R (version 3.0.1) using the package *vegan* (Oksanen *et al.* 2013). Diversity indices were computed as detailed above using self-developed software programmed in Python and C++ on a high-performance computing server with 32 CPU cores.

3.4.1.4 Results

ENMs were successful for 176 amphibian species. For the remaining 16 species point occurrences were too scarce, e.g. seven species are only known from their type locality. Overall, ENMs iterated on average 824 times (minimum: 80; maximum: 3240; standard deviation: 758) and performed well with an average AUC of 0.982 (min.: 0.882; max.: 0.999). All ENM parameters contributed to the models. On average the “total amount of precipitation” had the highest influence on individual ENMs, followed by the “wettest”, and the “driest month”. The variability of each parameters contribution is depicted in fig. 3.4.1-1. Details on the individual ENM results are summarised in the appendix (3.4.1-1). The individual ENM parameter contributions were used to map species relative to each

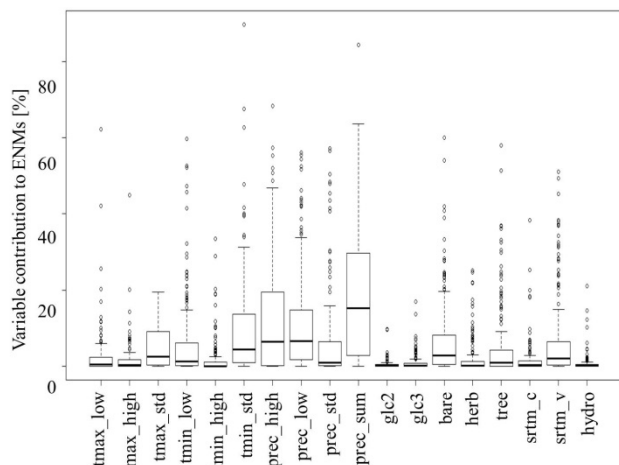


Fig. 3.4.1-1: Boxplots showing the variability of the contribution of each parameter (compare to tab. 3.4.1-1) to the 176 ENMs. All precipitation parameters apart from the standard deviation showed in general the highest contribution.

other using Nonmetric Multidimensional Scaling (NMDS) with the Morisita-Horn distance measure and 1,000 iterations. This visualises which species have similar niche spaces at least in terms of the parameter contribution of the calculated ENMs (fig. 3.4.1-2). The 18 environmental parameters in general separate the species well in ordination space. This is the first time that an almost complete (92%) and fine grained (30 arc seconds) map has been calculated for the amphibian diversity of West Africa (see fig. 3.4.1-3).

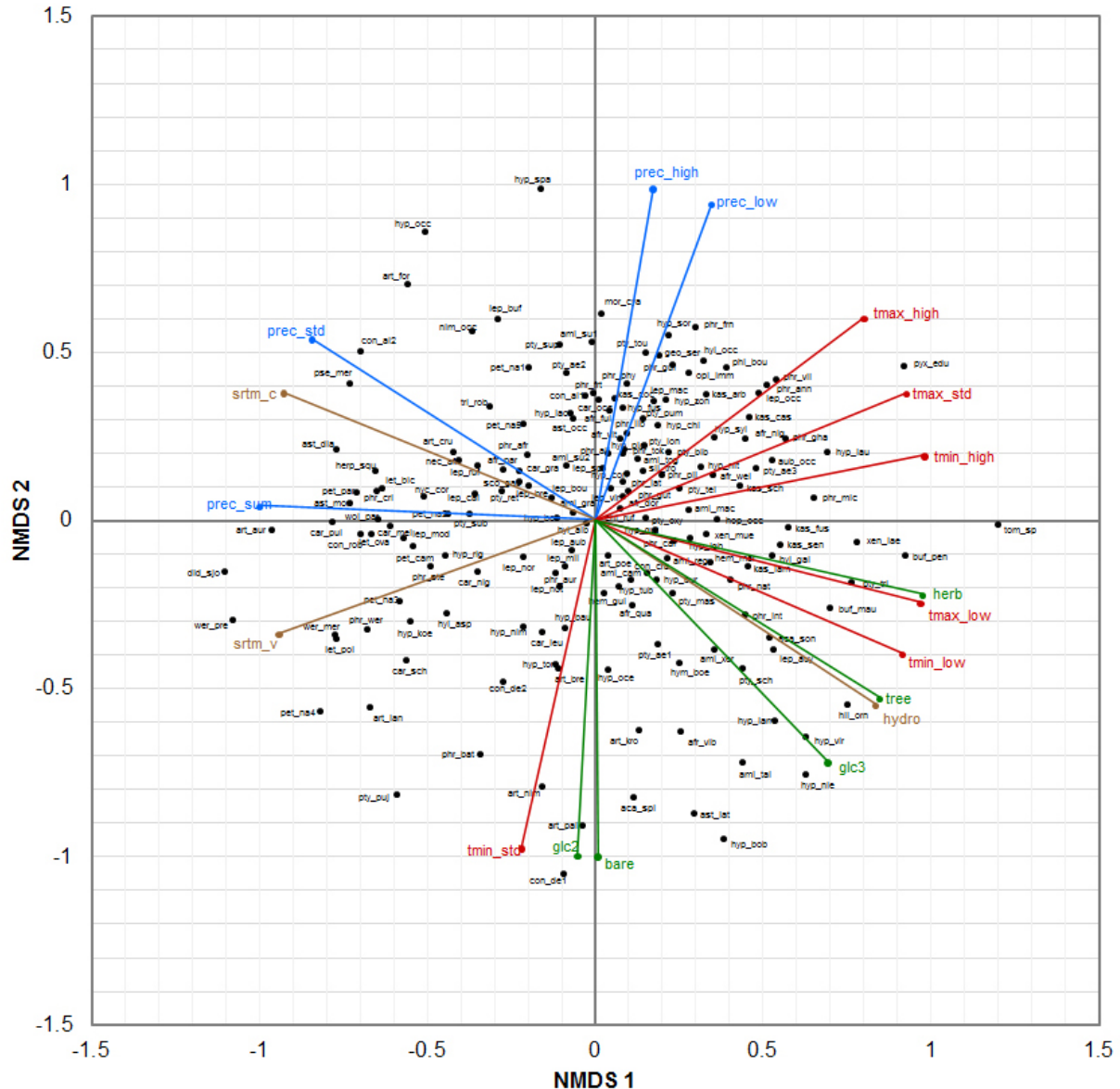


Fig. 3.4.1-2: NMDS using Morisita-Horn distance measures with 100 repetitions of the variable contributions per individual ENM. Species are coloured in black, ENM parameters and their vectors as follows (compare to tab. 3.4.1-1: temperature = red, precipitation = blue, environment = green; altitude & distance to river = brown. Parameters as well as species with similar contributions group together.

3.4.1.4.1 Distribution of diversity and unique taxa

Overall, regions of high species diversity were the foothills of the Cameroon Mountains which range into Nigeria. Within West Africa two main blocks were evident corresponding to two well-known ecoregions: Western and Eastern Upper Guinea forests (Burgess *et al.* 2004). Within the Eastern Upper Guinea forests both sides of the southern border between Cote d'Ivoire and Ghana harboured the highest species diversity. A number of patches of high diversity could be identified in the Western Upper Guinea forests. Exceptional areas were the Nimba Mountains

(border between Guinea, Liberia and Côte d'Ivoire), the western parts of Côte d'Ivoire (e.g. Mount Péko) and a large area in north-western Liberia, ranging into Sierra Leone and Guinea.

Interestingly, highlighted areas were almost identical, independent of the fact which subset of unique species was mapped:

- 1) endemic species (see figure 3.4.1-5a & app. 3.4.1-2; 81 (46%) species West African endemics; 62 (35%) Upper Guinea forest endemics)
- 2) threatened species (see figure 3.4.1-5b & 3.4.1-2; 67 (38%) species are threatened; category details are: 27 (15%) = "Near Threatened"; 16 (9%) = "Vulnerable"; 22 (13%) = "Endangered", = 2 (1%) = "Critically Endangered"; 7 (4%) = "Data Deficient" and 102 (58%) = "Least Concern")
- 3) evolutionary distinct species (ED) and evolutionary distinct and threatened (see figure 3.4.1-6a,b; Isaac *et al.* (2012) included 164 West African species, 154 of these corresponded to successful ENMs from our data set). The top ten ED species for West Africa and Upper Guinea endemics (and its combination with the Red List, EDGE) identified 30 different amphibians species (tab. 3.4.1-2). Within these 30 species, five species were consistently ranked high five times (*Arthroleptis aureoli*, *Arthroleptis cruscum*, *Conraua allenii*, *Conraua derooi* & *Pseudhymenochirus merlini*) and two species three times (*Nimbaphrynoides occidentalis*, *Phrynobatrachus annulatus*). The remaining 23 species were listed twice (7) or once (16).

The combination of criteria (endemic & threatened, endemic and ED, ED and threatened = EDGE) revealed similar pictures (app. 3.4.1-2. Thus, the areas of high diversity do not only harbour a large number of amphibian species but also a large number of unique (endemic, threatened and evolutionary distinct) species.

3.4.1.4.2 Coverage of protected areas

Our maps of the overall modelled diversity and the modelled distribution of unique species allow an indirect inference whether the spatial overlap of existing protected areas (PAs; fig. 3.4.1-4) is sufficient or not. It is important to note that the coverage does not include information on the situation on the ground and pinpoint for example so called "paper parks" (Carey *et al.* 2000). Overall some areas are well covered by PAs (the Nimba region, western Côte d'Ivoire, south-western Ghana and the Nigerian part of the Cameroonian Highlands). Other areas need to be carefully evaluated for improvements in the protected area network such as south-eastern Côte d'Ivoire, parts of Liberia, particularly in the north-west, parts of Sierra Leone and parts of Guinea (compare figs. 3.4.1-3a,b and 3.4.1-4).

3.4.1.4.3 Methodological approach

Spatial filtering was imbedded in our workflow after conducting the ENMs in order to further improve the biogeographical relevance. The influence of the spatial filtering on the distribution pattern is obvious from the comparison of 3.4.1-3a (with spatial filter) and figs. 3.4.1-3c (without spatial filter). Both figures show the log transformed spatial distribution of the alpha diversity. In general, the same centres of importance were highlighted. However, a much higher diversity was depicted in the Nigerian lowland forests and in the Western Upper Guinea forests. The ENMs predicted several species to occur there but current expert opinion shows that they are up to now absent from the area in many cases replaced by ecologically similar species. The mapped diversities revealed a small difference in the highlighted areas between the two indices used, simple taxon richness and the "true" alpha diversity (after Jost 2007). However, overall the same centres of high modelled amphibian diversity areas were delineated.

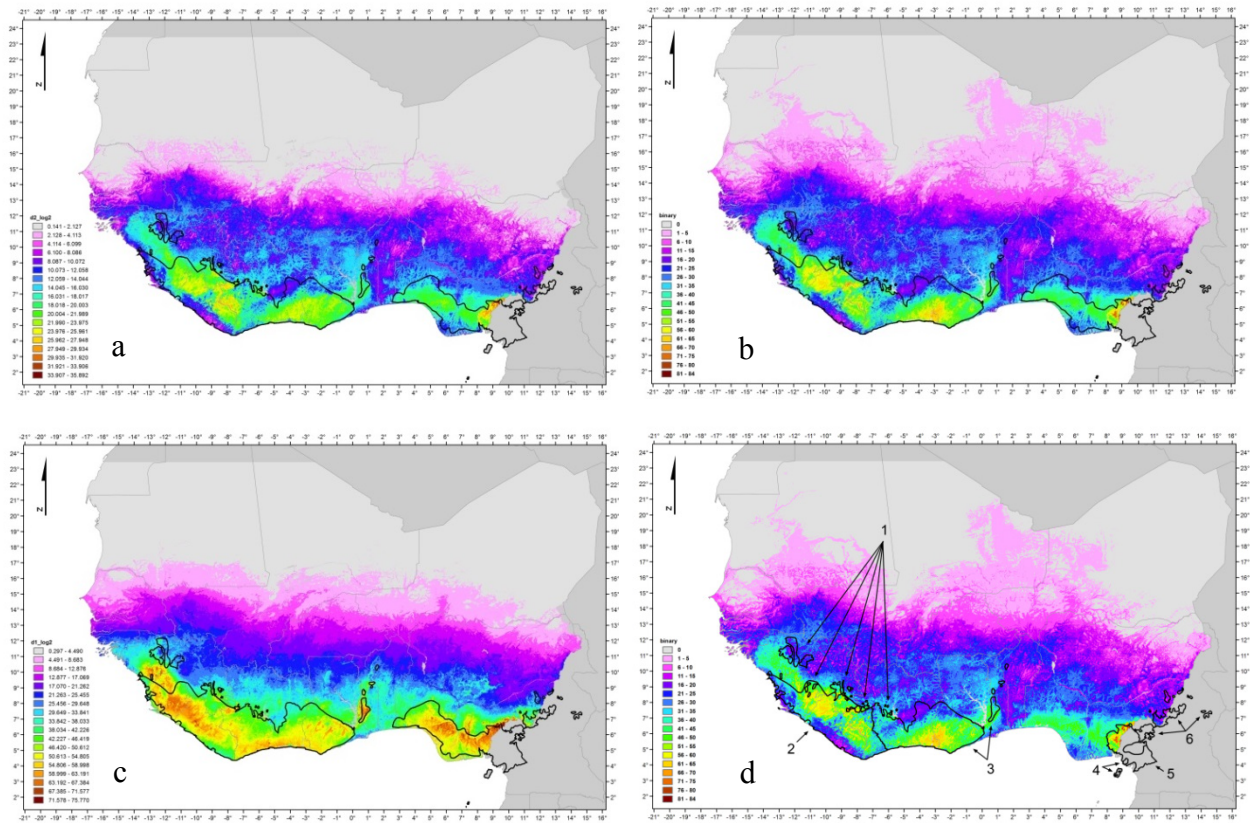


Fig. 3.4.1-3: Maps of modelled amphibian diversity in West Africa for 176 species, state boundaries are coloured in dark grey, the regional extent in light grey and the delineation (black line) of the hotspot “Upper Guinea forests” (after Mittermaier *et al.* 2004). In detail a) shows log transformation of the exponential Shannon richness for spatially filtered data (alpha diversity); b) the richness of the binary data; c) the log transformation of the exponential Shannon richness for data not spatially filtered, hotspot as in a; d) the same binary richness as in b with the delineation of the different ecoregions (after Burgess *et al.* 2004), 1 = Guinean montane forests, 2 = Western Guinean forests, 3 = Eastern Guinean forests, 4 = Mt. Cameroon & Bioko montane forests, 5 = Cross-Sanaga-Bioko Coastal forests, 6 = Cameroon highland forests. Further maps are found in the app. 3.4.1-2.

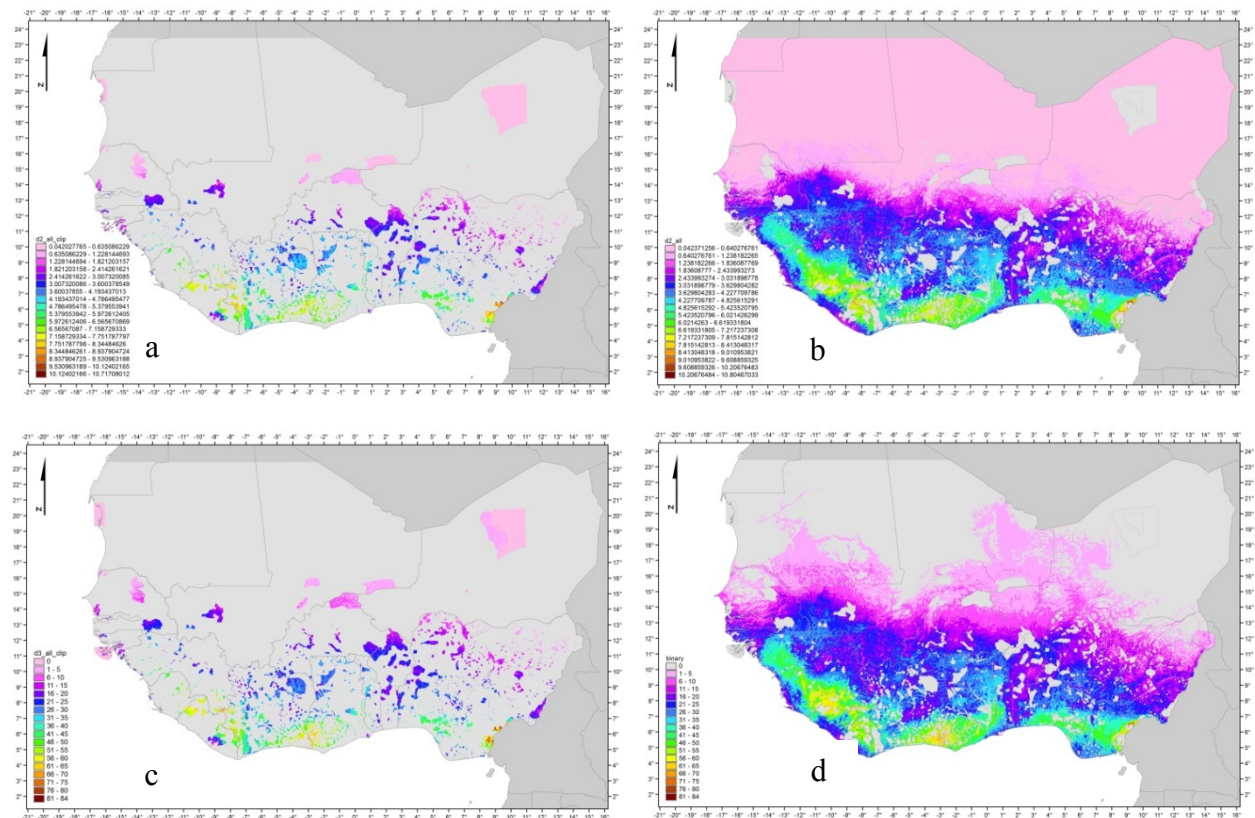


Fig. 3.4.1-4: Maps of modelled amphibian diversity and their spatial overlap with the existing protected area network. The left column (a & c) depicts the diversity inside the right one (b & d) outside the PAs. The top row shows the transformed Shannon diversity, the bottom one the binary species richness.

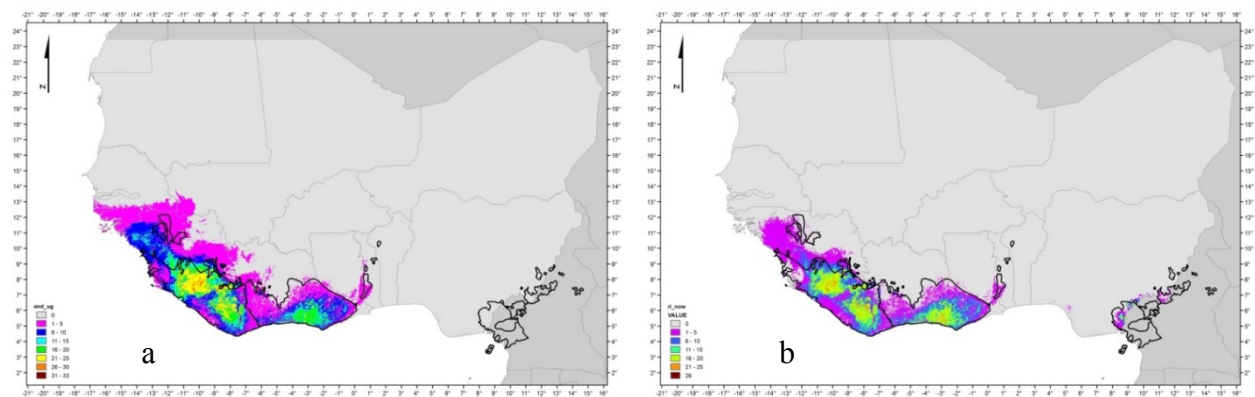


Fig. 3.4.1-5: Binary species richness of species endemic to the Upper Guinea forests (a) and species classified as threatened on the IUCN Red List (b). Ecoregion delineation (black lines) is as in 3.4.1.3d.

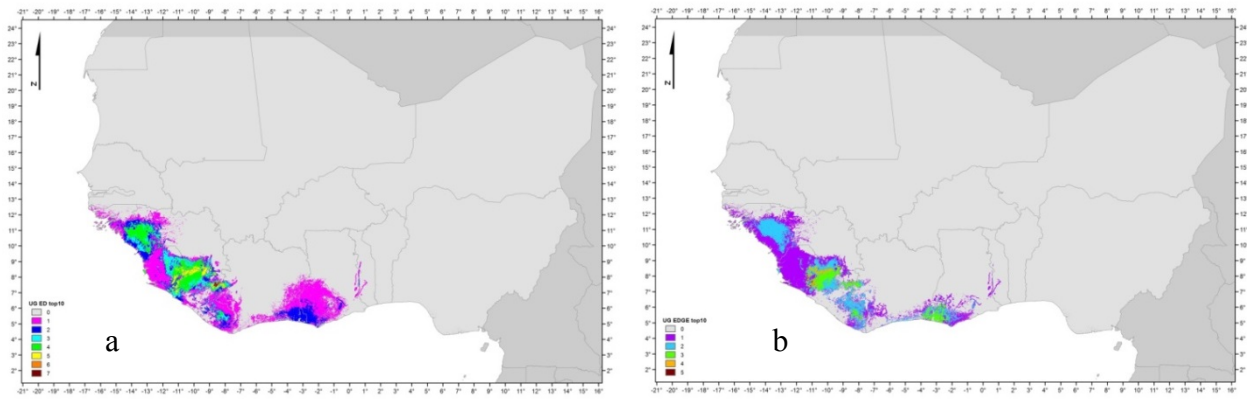


Fig. 3.4.1-6: Binary richness of the top ten ranked species according to the ED score (a) and the EDGE score (b) (from Isaac *et al.* 2012) which are endemic to the Upper Guinea forests.

Tab. 3.4.1-2: Ten highest ED and EDGE scores for the whole data set ($n = 176$) and for the West African ($n = 81$) and Upper Guinea forest endemic ($n = 62$) species respectively.

#	All	ED	#	All	EDGE
1	<i>Pseudhymenochirus merlini</i>	73.77687	1	<i>Conraua derooi</i>	6.11896
2	<i>Herpele squalostoma</i>	73.16651	2	<i>Nimbaphrynoides occidentalis</i>	5.03328
3	<i>Geotrypetes seraphini</i>	59.42539	3	<i>Arthroleptis aureoli</i>	5.02566
4	<i>Scotobleps gabonicus</i>	56.28777	4	<i>Cardioglossa melanogaster</i>	5.02566
5	<i>Hymenochirus boettgeri</i>	53.73178	5	<i>Cardioglossa pulchra</i>	5.02566
6	<i>Nyctibates corrugatus</i>	38.13391	6	<i>Cardioglossa schioetzi</i>	5.02566
7	<i>Trichobatrachus robustus</i>	37.09279	7	<i>Arthroleptis cruscum</i>	4.91817
8	<i>Silurana tropicalis</i>	32.90127	8	<i>Didynamipus sjostedti</i>	4.87814
9	<i>Opisthothylax immaculatus</i>	31.71966	9	<i>Leptodactylodon bicolor</i>	4.78715
10	<i>Petropedetes cameronensis</i>	30.72404	10	<i>Conraua alleni</i>	4.73267
#	West Africa endemics	ED	#	West Africa endemics	EDGE
1	<i>Pseudhymenochirus merlini</i>	73.77687	1	<i>Conraua derooi</i>	6.11896
2	<i>Petropedetes natator</i>	30.37771	2	<i>Nimbaphrynoides occidentalis</i>	5.03328
3	<i>Conraua derooi</i>	27.39963	3	<i>Arthroleptis aureoli</i>	5.02566
4	<i>Conraua alleni</i>	27.39963	4	<i>Arthroleptis cruscum</i>	4.91817
5	<i>Pyxicephalus edulis</i>	21.81476	5	<i>Conraua alleni</i>	4.73267
6	<i>Astylosternus occidentalis</i>	18.33349	6	<i>Phrynobatrachus annulatus</i>	4.67711
7	<i>Arthroleptis aureoli</i>	18.03378	7	<i>Phrynobatrachus ghanensis</i>	4.67711
8	<i>Arthroleptis nimbaensis</i>	16.09402	8	<i>Amietophrynus taiensis</i>	4.41937
9	<i>Arthroleptis cruscum</i>	16.09402	9	<i>Hylarana occidentalis</i>	4.34738
10	<i>Arthroleptis brevipes</i>	16.09402	10	<i>Pseudhymenochirus merlini</i>	4.31451
#	Upper Guinea endemics	ED	#	Upper Guinea endemics	EDGE
1	<i>Pseudhymenochirus merlini</i>	73.77687	1	<i>Conraua derooi</i>	6.11896
2	<i>Petropedetes natator</i>	30.37771	2	<i>Nimbaphrynoides occidentalis</i>	5.03328
3	<i>Conraua alleni</i>	27.39963	3	<i>Arthroleptis aureoli</i>	5.02566
4	<i>Conraua derooi</i>	27.39963	4	<i>Arthroleptis cruscum</i>	4.91817
5	<i>Astylosternus occidentalis</i>	18.33349	5	<i>Conraua alleni</i>	4.73267
6	<i>Arthroleptis aureoli</i>	18.03378	6	<i>Phrynobatrachus annulatus</i>	4.67711
7	<i>Arthroleptis brevipes</i>	16.09402	7	<i>Phrynobatrachus ghanensis</i>	4.67711
8	<i>Arthroleptis cruscum</i>	16.09402	8	<i>Amietophrynus taiensis</i>	4.41937
9	<i>Arthroleptis nimbaensis</i>	16.09402	9	<i>Hylarana occidentalis</i>	4.34738
10	<i>Leptopelis macrotis</i>	15.00707	10	<i>Pseudhymenochirus merlini</i>	4.31451



3.4.1.5 Discussion

Environmental Niche Models (ENMs) are usually either based on a global data set, thus using a coarse scale (e.g. 1° grid cells which is ca. 111x111km at the equator) or in the case of finer scales investigating temperate regions (e.g. Cayuela *et al.* 2009). Herewith, we present for the first time a subcontinental fine grained (30 arc seconds = ca. 1x1km) diversity maps for a nearly complete set of tropical amphibians, which due to its higher resolution does in particular provide an adequately fine grained baseline information for conservation decisions (see Warman *et al.* 2004; Shriner *et al.* 2006; Hurlbert & Jetz 2007; Jetz *et al.* 2007).

3.4.1.5.1 Distribution of diversity

Our modelling approach identified several centres of high amphibian diversity. The main areas are south-western Sierra Leone and north-eastern Liberia, the Nimba Mts., south-western Ivory Coast and south-eastern Ghana and the Nigerian part of the Cameroon highlands (see fig. 3.4.1-3). These centres of high diversity are generally situated in areas of remaining lowland forests and or of higher altitudes, with rivers acting as main barriers (see fig. 3.4.1-7 and Penner *et al.* 2011).

Comparison with other studies are challenging because no comparative study exist. Nevertheless, cautious comparisons are possible if the differences in scale, extent, methodological approaches and changes in taxonomy between other papers and thus study are kept in mind.

Amphibians have been assessed on a global scale using a hexagonal grid (ca. 0.5° diameter in West Africa). Overall diversity was grouped only roughly and identified the Upper Guinea forests as an area of highest diversity. No finer patterns were mapped. Mapping of Red List species pointed to three regions: Nimba Mts. an area around Tai NP and south-western Ghana (IUCN 2013). Thus, our highlighted areas in Liberia, Sierra Leone and Guinea as well as the Nigerian parts of Cameroon highlands were missing. An analysis of West African amphibian assemblages found that the Nimba Mts., Pic de Fon and the Tai NP held highest diversities (Penner *et al.* 2011). An older analysis used much coarser regions but did consistently rank the “Guinean block” as part of the province “Western” within the region “Western Equatorial”. Ranks (out of 28) were 2nd place for species numbers, 3rd place for genera numbers, 10th place for endemic species and 14th place for endemic genera (Poynton 1999). No smaller scaled patterns were identified. Assessing distribution patterns of hyperolid frogs (reed frogs), Schiøtz (1967) already hinted towards the Nimba Mts. as an area of high diversity.

Geographical extrapolations of other species take no coherent line. In many coarse studies no real pattern was identified for the overall diversity in West Africa (mammals: Hacker *et al.* 1998; birds: Jetz & Rahbek, 2002; Orme *et al.* 2005; Grenyer *et al.* 2006). Other analyses revealed a high diversity either in the forest biomes (mammals: Hacker *et al.* 1998; small range birds: Jetz & Rahbek 2002; <25% of all as well as of “Near Threatened” reptile species: Böhm *et al.* 2013), the savannahs (large range birds: Jetz & Rahbek 2002) or in the forest-savannah transition zone (mammals: Grenyer *et al.* 2006; Thuiller *et al.* 2006; Rondinini *et al.* 2011; IUCN 2013; birds: Williams *et al.* 1999; large range birds: Jetz & Rahbek 2001). The Upper Guinea forests were often consistently identified as one zoological region (birds: De Klerk *et al.* 2002a; rare & endemic birds: Grenyer *et al.* 2006; fish: Hugueny & Lévêque 1994; vascular plants: Barthlott *et al.* 2005). Interesting differences are for example that fish assemblages showed a biogeographic border different to amphibians, namely the Cavally river, between Western and Eastern Upper Guinea forests (the latter called “Eburneo-Ghanean”; Hugueny & Lévêque 1994). Our study identified the Banama river (equivalent to the V Baolé) as the major border between the two regions. Furthermore, data from vascular plants indicated highest West African diversity at higher elevations, i.e. around the Nimba Mts., ranging east to Mt. Peko and westwards into Sierra Leone. In addition the “Nigerian lowland forest” contained similarly high plant diversity (Barthlott *et al.* 2005). Contrastingly, our amphibian data shows a relatively low diversity for the “Nigerian lowland forests” in the spatially filtered data sets (b & c). A third region identified by Hugueny & Lévêque (1994, fish), the “Lower Guinea forests” did not include the

Cross river and the Nigerian parts of Cameroon highlands but only the areas east and south of them. Our amphibian data suggest the inclusion of the latter two areas in the region. The centres of high diversity are also often centres of high endemism (e.g. fish; Hugueny & Lévêque 1994). Finer regional details were (for birds) that the Nimba Mts., Taï NP, south-western Ghana were areas of high diversity. Areas of high endemism were the same areas plus the southern border between Togo and Ghana, Pic de Fon and roughly the Guinean border to Liberia, Sierra Leone (De Klerk *et al.* 2002a & b).

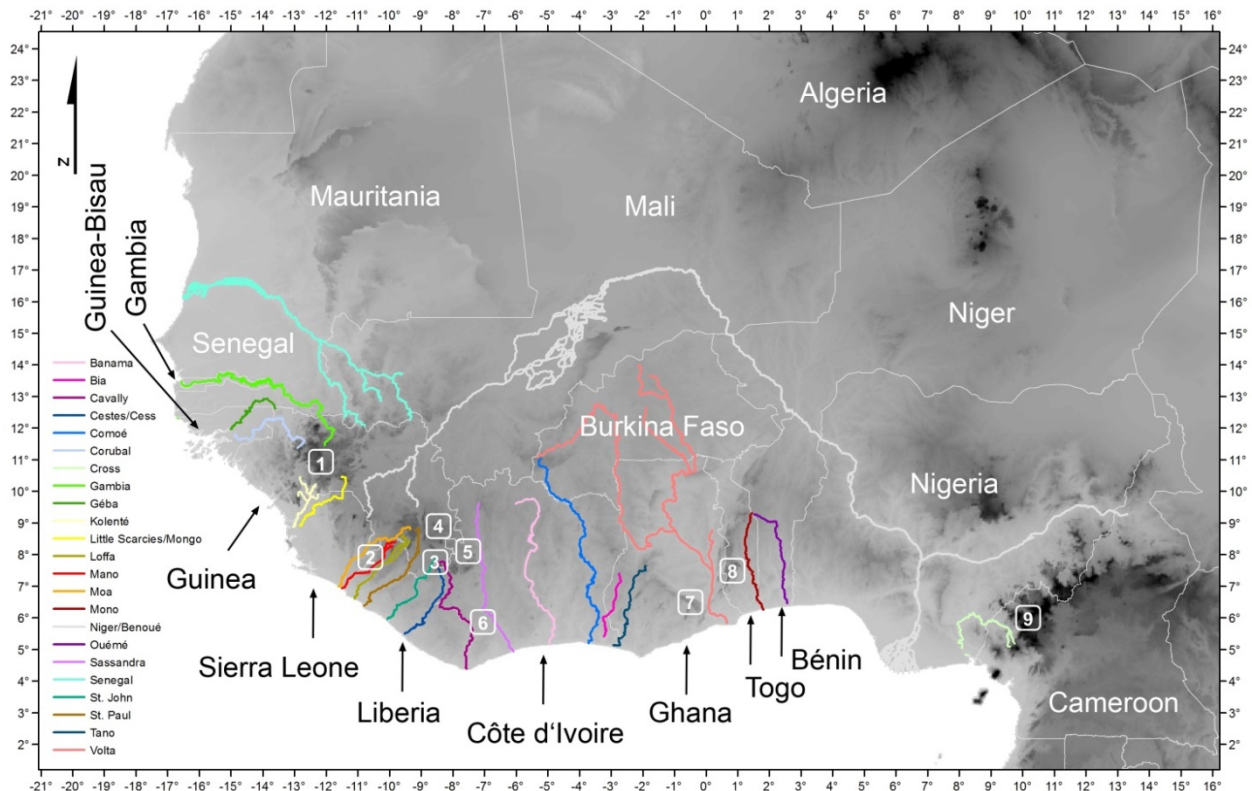


Fig. 3.4.1-7: Map showing biogeographical barriers in West Africa and the relevant countries. Rivers are colour coded as detailed in the legend. The location of biogeographically important areas (discussed in the text) are indicated by their numbers: 1 = Fouta Djallon, 2 = Gola forest, 3 = Nimba Mts., 4 = Simandou range, 5 = Mt. Péko National Park, 6 = Taï National Park, 7 = Atewa range, 8 = Togo highlands, 9 = Cameroon highlands. Altitude is depicted in grey on a 150 arc seconds grid derived from an ASTER data with the maximum altitude at 5412m a.s.l. (black)

3.4.1.5.2 Pleistocene refugia

The areas of high diversity are also important from a historical and evolutionary point of view. Past glacial periods lead to an alternating wet and dry climate in West Africa and the areas of high diversity remained a relatively stable climate over time, therefore gained highly diverse communities over time. Thus areas of high diversity are thought to be Pleistocene refugia (e.g. Diamond & Hamilton 1980, Crowe & Crowe 1982, Mayr & O'Hara 1986, Grubb 1992). Currently three to four coarse Pleistocene refugia have been defined for West Africa, corresponding to Western and Eastern Upper Guinea forests ecoregions and the Nigerian part of the Cameroon highlands. The Western Guinea forests are sometimes separated in two refugia (see also Penner *et al.* 2011 and references therein). Another possibility of inferring Pleistocene refugia, is to compare the ENMs of the most evolutionary distinct (ED) to the general modelled amphibian diversity. We took the ten highest ranked taxa and the overall pattern does not change but the core areas move, emphasising the Nimba Mts. and areas in north-western Liberia and south-eastern Sierra Leone even more. In summary, our data confirms the rough pattern but does indicate more and smaller potential Pleistocene refugia (see chapter 3.2).

3.4.1.5.3 Unique species

Partitioning of the data set and mapping of unique amphibian subsets -endemic, threatened, ED or combinations of these three groups - highlighted similar but not always identical areas. For example, mapping the ED and EDGE Upper Guinean endemics, identified two important areas: the Nimba Mts. and the neighbouring areas along the borders between Guinea, Liberia and Sierra Leone for ED scores and the forests around Gola NP plus similar areas in Sierra Leone, forests in eastern Liberia as well as forests in south-eastern Côte d'Ivoire/south-western Ghana for EDGE scores (see figure 3.4.1-6a & 3.4.1-6b). The Nigerian parts of the Cameroon highlands came out very prominently in all approaches.

The main result from the different partitions is that the areas of high diversity are also the areas where unique species occur. This has two important implications. Firstly, from a biogeographic point of view it supports the notion that areas of high diversity present Pleistocene refugia. Secondly, for conservationists it means that conserving a high amphibian diversity, protects threatened, endemic and evolutionary distinct species at the same time.

3.4.1.5.4 Linking amphibian diversity & forests

The distribution pattern visible from the maps is derived from the ENM parameters. The parameter describing the total amount of precipitation was the main ENM parameter. Thus individual ENMs and overall diversity are dependent on rainfall patterns. At the same time the link between the distribution of lowland tropical forests and rainfall is also well established (Porter *et al.* 2004) leading to a direct correspondence between the standing forests (Bongers *et al.* 2004) and areas of high amphibian diversity. This clearly emphasises the conservation importance of the remaining primary forests in West Africa.

However, the question might arise if this situation really holds true on the ground in West Africa with large tracts of forest already gone, the remaining forests being heavily fragmented and in many instances disturbed (see Mayaux *et al.* 2005, 2013; Hansen *et al.* 2008)? We argue that this situation holds true and is supported by a number of arguments. For example in Mexico, even small fragments, but >17ha, can support a similar herpetofauna as large tropical forests (Cabrera-Guzmán & Reynoso 2012). In Ghana, diversity of leaf litter frogs is preserved in secondary and selectively logged forests (Ofori-Boateng *et al.* 2012; Adum *et al.* 2013). Even, in case frog diversity is lost, it can recover. It was shown that around 20 years after selective logging at a low intensity rate (≤ 3 trees/ha) leaf litter frog diversity recovered in a mosaic of used and non-used forests (Adum *et al.* 2013). More generally, recovery rate naturally depends on the degree of disturbance, thus in more severe cases does take much longer. Estimates state that a couple of centuries (100 to 500 years or more) might be required for tropical lowland forests (see review by Chazdon 2003). The threat situation becomes even more complex. Studies from neighbouring Côte d'Ivoire showed that diversity alone might not always be a good measurement. There fragmentation did not change species richness but altered functional diversity, meaning that species which are highly dependent on forests disappear and are replaced by more common species invading from farm-bush and savannah regions (Ernst & Rödel 2005; Ernst *et al.* 2006, Hillers *et al.* 2008c).

The overall evidence clearly states that primary forests not only in West Africa but throughout the globe are the only places where overall tropical diversity can be maintained (Gibson *et al.* 2011).

3.4.1.5.5 Conservation

In general, considering various taxa and different criteria, a number of different concepts have been put forward to identify areas of special biological/conservation importance and therefore assist in global prioritisation schemes (see review by Brooks *et al.* 2006). In the following we will compare our results against the two most commonly used global concepts hotspots (Myers 1988, 1990; Myers *et al.* 2000; Mittermeier *et al.* 2004) and terrestrial ecoregions (Burgess *et al.* 2004), as well as against the current network of protected areas in West Africa.

Overlaying the hotspots and the ecoregions with our modelled amphibian diversity, it is evident that regardless which coarse concept is used, our finer scale reveals several areas of importance within the global ones (see fig. 3.4.1-3d). Thus, in order to prioritize conservation at the manageable small conservation scale the data has to meet that scale. In detail our results show two main differences between the ecoregions and our results: the western edge of the Western Upper Guinea forests and the mountains of the Fouta Djallon. Both areas are included in the respective ecoregion but their inclusion is not supported by our amphibian data.

Detailing the fine grained pattern and extrapolating into the distributional gaps between occurrence records provides decision makers with needed data. These data can serve several purposes, e.g. can guide decision makers to areas where verification of the predicted diversity is needed. In our case mainly sites in Guinea and Sierra Leone, but also in lowland forests of Liberia and Nigeria. Likewise, our data tests whether areas of high amphibian diversity are covered by existing protected areas (figs 3.4.1-4 & app. 3.4.1-2). In many instances areas of high amphibian diversity fall within protected areas. However, many of these are so called “classified forests” (“forêts classées”) (app. 3.4.1-3) which means that some degree of utilisation is allowed). Unfortunately, in many cases no control exists and protected areas do only exist on paper but are not protected in reality (compare to Kouame *et al.* 2012). The lack of law enforcement is especially worrying because many of these protected areas are irreplaceable (see Rondinini *et al.* 2006) and do provide benefits to the local people (Larsen *et al.* 2012). Furthermore, our results point to areas where potentially new protected areas are required. In particular, these are south-western Côte d'Ivoire, north-western Liberia and the connecting areas in Sierra Leone and Guinea (fig. 3.4.1-4 & app. 3.4.1-2).

The remaining protected and unprotected forests in West Africa are under enormous pressure. They are heavily fragmented (Wegmann 2009), in many places destroyed and large tracts (> 80%; Norris *et al.* 2010) have already been gone (see also Mayaux *et al.* 2005; Hansen *et al.* 2008; Mayaux *et al.* 2013). Main pressures are small scale farming (Hansen *et al.* 2008) but also more recently logging concessions of large companies, which have lately acquired more than 60% of Liberia's remaining forests (Global Witness Report 2012) though these are the largest persisting forest blocks. In addition, mining plans enhance the tension further (e.g. see Intierra Mapping 2008, 2009, 2010, 2011, 2012, 2013). The pressures on the forests in West Africa will certainly increase even more in the near future. Not only are administrations on different levels having difficulties to stop habitat degeneration and loss but an increasing threat will be climate change. Climate change will accelerate the situation and in turn will be fuelled by the on-going changes (Campbell *et al.* 2009).

Our data and reasoning all support the demand that the remaining forests in West Africa have to be protected from further destructions. This has to take two paths: ensuring that already existing PAs are also protected in reality and that new PAs are declared in order to protect more diversity in the remaining forests and provide important links (stepping stones and corridors) in the existing PA network.

3.4.1.5.6 Methodology

Finally we would like to discuss two methodological aspects shortly. Firstly, the choice of measurement: the differences between using the “true” alpha diversity (after Jost 2007) and simple species richness were small. Overall, the same general areas were depicted with only minor shifts of local diversity centres inside these areas (fig. 3.4.1-3a vs. 3.4.1-3c). Secondly, the effect of spatial filtering: very contrasting results were obtained when spatial filtering was excluded and our results underline the importance of this approach for our data set. Currently we are aware of two methods applying spatial filters: either introducing them in the ENMs (see De Marco *et al.* 2008, Blach-Overgaard *et al.* 2010) or correcting ENMs afterwards via expert opinion as described in this paper. The first approach is more general but spatial filters have to be defined beforehand, thus practicability limits the number of spatial filters and currently is only used for coarse scales (100 by 100km; slightly less than 1°; Blach-Overgaard *et al.* 2010). Our approach is more applicable to fine grained data and treated every taxon individually. Whatever the spatial filtering approach is, we clearly recommend using one. For example in our data set

the ecoregion “Nigerian lowland forests” showed a high amphibian diversity, comparable to all other high diversity areas when no spatial filters were applied (fig. 3.4.1-3c). However, spatial filtering, based on field data from these forests, corrected values to a much lower overall prediction (see fig. 3.4.1-3a). It remains to be tested how the importance of spatial filtering will change with ENM grain size (resolution). From a conservation point of view it seems that data which most closely reflects reality, e.g. achieved through spatial filtering, is more important than choosing the right diversity measurement.

3.4.1.5.7 Summary

Our work should be seen as supplemental to broad scale biogeographical conservation approaches (e.g. Linder *et al.* 2012, Safi *et al.* 2013), confirming the rough diversity pattern, including unique species, and supplying the finer scale details. Herewith we also confirm that the main separators between areas of high amphibian diversity within West Africa are rivers because some of them correspond well with drop offs in species diversity and ecoregion borders (see fig. 3.4.1-7; see Penner *et al.* 2011).

We showed that several distinct hotspots of amphibian diversity exist within West Africa. We likewise could confirm, at a much higher resolution, previous studies showing a clear division between West and Central Africa amphibian diversity (Schlötz 1967, 2007; Penner *et al.* 2011). Furthermore we back up the distinction, meaning the occurrences of different species, between Western and Eastern Upper Guinea forests. Conservation in the region, as elsewhere in the world, is associated with a number of complex problems which are not easily solvable. Nevertheless, our data clearly supports the need for a well-designed, properly functioning PA network to conserve as much of the remaining forests their amphibian diversity and uniqueness as possible.





3.4.2 Keep it simple? Dispersal abilities can explain why species ranges differ

3.4.2.1 In a nutshell



A well-known positive correlation between niche breadth and range size exists across a number of animal and plant taxa. A relatively more simple explanation, range size being connected to differing dispersal abilities, was recently presented for passerine birds. Unfortunately, respective datasets are not easily available for other taxonomic groups.

We circumvented this problem by developing a simple dispersal index, incorporating niche information (body size, litter size, preferred habitats of adults and offspring, ecotype of adults) which can be collected straightforwardly for most animal taxa. We tested this dispersal index for species generally considered poor dispersers, amphibians. Our results revealed a positive correlation between the dispersal index and range size ($p < 0.001$).

Our index can easily be transferred to and tested with other taxa. Furthermore, our results suggest the integration of information on dispersal abilities in niche modelling processes which assess the impact of climate change on future species distributions.

3.4.2.2 Introduction

The niche of a species is generally described as a hyperdimensional space, comprising all environments and resources which influence its survival and performance (Hutchinson 1957) and which are in turn influenced by the species (Leibold 1995; see also Chase & Leibold 2003 for a recent review and refinement of the niche concept). The hypothesis that species with broader niches should have larger geographic ranges was already reviewed nearly 30 years ago (Brown 1984) and recently confirmed across a wide range of animal and plant taxa (Slatyer *et al.* 2013). However, the niche of a species is determined by a large variety of different abiotic and biotic factors, the interactions between these factors and with the species, and all may act on different spatial and temporal scales. In addition, large intraspecific variations may occur in the direction and strength of certain factors (Morrison & Hero 2003). Therefore, the niche of a species is a complex concept which is difficult to measure unambiguously. Thus, it is not surprising that the generalisation that there is a positive correlation between niche breadth and geographical range was not universally accepted (see Slatyer *et al.* 2013).

Nevertheless, the discussion why some species do have larger range sizes than others is still on-going and earlier studies have discussed a variety of less complex explanations than niche breadth, investigating only parts of the niche, e.g. dispersal ability (see Lester *et al.* 2007). However, the same paper failed to find evidence for a relationship between range size and dispersal ability in various marine taxa. One major problem of studies investigating dispersal abilities is that comprehensive data is often lacking because no universal measurement of dispersal ability exists; neither across nor even within most taxonomic groups. A number of indirect measures to assess dispersal have been used, e.g. distance travelled (e.g. Spieler & Linsenmair 1998), genetic exchange (e.g. Szymura & Barton 1991) and evolutionary time (e.g. Pigot *et al.* 2012, see also review by Smith & Green 2005).

The rare exception in this general lack of knowledge on dispersal are birds, where individual marking, in the form of ringing, has a long tradition, spanning large geographic areas and numerous taxa, amounting in decades of data (e.g. see Laube *et al.* 2013). An exceptional dataset of European passerine birds showed that dispersal ability, measured as the ratio between Kipp's distance ("distance between the tip of the first primary to the tip of the wing") and bill depth (height at base), has an influence on the species' range sizes (Laube *et al.* 2013); meaning that birds with a better dispersal ability have larger distribution ranges. However, although birds do have ideally suited data sets they are also exceptional dispersers due to their ability to fly, making dispersal comparatively easier for them than for other groups. We are not aware of similar comprehensive data sets for any other group of animals. Furthermore, the study by Laube *et al.* (2013) also exemplifies a major bias in the existing dispersal literature: the majority of studies deal with endotherms and temperate regions (Europe or North America).

Lead by the corroboration that in general niche breadth and range size are positively linked (see Slatyer *et al.* 2013), as well as the findings that dispersal ability provided a more frugal explanation for range-sizes in passerine birds (see Laube *et al.* 2013), we herein developed a simple universal measure of dispersal ability and investigated the question whether there is a correlation between this index of dispersal abilities and range sizes? In particular, if one investigates tropical, non-volant ectotherms, which exhibit a high degree of habitat specificity and due to a number of other characteristics, are generally considered having poor dispersal abilities. To test this question we used a comprehensive data set of niche characteristics of West African amphibians, which revealed that their dispersal abilities are positively correlated with range sizes.

3.4.2.3 Material & Methods

3.4.2.3.1 Amphibian data

Our geographic region is a well-defined African biome and its definition included all countries west of Cameroon and south of the Saharan desert, herein termed West Africa (see Penner *et al.* 2011). We used a dataset of West African amphibians where taxonomic work over the last two decades resolved potential taxonomic issues and resulted in a total of 192 validated taxonomic units which are either described species or considered confirmed candidate species (compare to Vieites *et al.* 2009). For the present work, environmental niche models (ENMs) were calculated for 176 of these taxa (see app. 3.4.2-1).

3.4.2.3.2 Dispersal ability index

Amphibians are generally considered having low dispersal abilities (e.g. Sinsch 1990; Blaustein *et al.* 1994; Duellman & Trueb 1994) but probably with high interspecific variation (e.g. Marsh & Trenham 2001). Overall, data on dispersal abilities for amphibians are scarce and have to be gathered via extensive and expensive methods. For West Africa data exists only for two species (*Hoplobatrachus occipitalis*; Spieler & Linsenmair 1998 and *Phrynobatrachus guineensis*; Sandberger *et al.* 2010). It is impossible to gather such data for the majority of species within a reasonable time. Therefore an indirect measure has to be used. We collected niche characteristics for all taxonomical units (n = 176; see 3.4.2-1), consisting of a variety of measured and estimated parameters which we considered essential for the dispersal abilities and which were easy to collect.

3.4.2.3.2a Snout-vent length [SVL; measured in millimetres]

Larger frogs are less vulnerable to predation (Chelgren *et al.* 2008), desiccation (e.g. Jameson 1956; Semlitsch 1981; Rothermel & Semlitsch 2002) and travel larger distances (Goater *et al.* 1993; Beck & Congdon 2000). Thus, larger frogs should have dispersal advantages. The assumption that dispersal is not uniform, e.g. juveniles (e.g. Dole 1971; Breden 1987; Berven & Grudzien 1990), males (e.g. Lampert *et al.* 2003) or females (e.g. Austin *et al.* 2003; Palo *et al.* 2004) being the main dispersal life stage, remains untested for West African species. For most species it remains also unknown at which age they start reproducing, thus the distinction between juveniles and adults is not always straightforward. Therefore, the mean SVL of adults can be seriously hampered by the inclusion of small, possibly immature frogs. To avoid that, we recorded only the maximum sizes for males and females. The dispersal index used the size of the larger sex (usually the female).

3.4.2.3.2b Clutch size [CI; assigned to six categories]

We recorded the number of eggs a single female may deposit during one breeding event either from own data or from the literature. Clutch sizes were grouped in four categories < 20 eggs (i), 21-100 (ii), 101-1000 (iii), > 1001 (iv). For reasons of simplification, we assumed that predation on eggs and tadpoles are comparable throughout species and thus having larger clutches is a dispersal advantage. The four categories were taken into account by integrating the multiplication factor of 1 (i), 2 (ii), 3 (iii) and 4 (iv), respectively into the dispersal index.

3.4.2.3.2c Preferred habitat of adults [Ad-Hab; six categories]

The habitat preferences of adults for all species were assigned to six categories: primary forests (PF), secondary forests (SF), forest edges and clearings (FE), highland savannahs (HS), lowland moist savannahs (LSM) and lowland dry savannahs (LSD); multiple assignments were possible. Forests, both primary and secondary, are heavily fragmented in West Africa and very few large forest patches still persist (e.g. Mayaux *et al.* 2004; Hansen *et al.* 2013). We assumed that forest dependent species very rarely cross savannahs, whereas savannah species can cross forested habitats along roads and other anthropogenic openings or even move within forest. The latter is supported by data which revealed savannah species deep inside rainforest, on so called inselbergs (Schorr 2003). In West Africa, highland savannahs are naturally fragmented. Thus FE, LSM and LSD were included in the dispersal index with the multiplication factor two, PF, SF and HS with the factor one.

3.4.2.3.2d Preferred ecotype of adults [EcoT; four categories]

Species were classified in four categories: terrestrial, arboreal, fossorial and aquatic. We assumed that terrestrial amphibians have a dispersal advantage over the remaining three classes because their habitat is, relatively seen, more “continuous” than for the other three categories. Therefore, this category received a multiplication factor of two, while the others received one of one.

3.4.2.3.2e Larval habitat [L-Hab; five categories]

The habitat preferences of amphibian larvae, tadpoles, were assigned to five categories related to their dependence on water: terrestrial (i; including life birth) and stagnant permanent (ii), stagnant temporary (iii), flowing lowland (iv), flowing mountain (v) aquatic habitats. We considered the first three categories (i, ii & iii) as facilitating dispersal and the remaining two as limiting dispersal. The reasoning was that suitable breeding habitats are generally scarce, giving a dispersal advantage to species who are independent of water (i) and who can use the most abundant water bodies – stagnant ponds (ii & iii), at least during the rainy season and in our study area. Smaller flowing waters may dry out in drier areas, larger ones may contain predatory fish and both are less abundant than stagnant waters. Thus, the facilitators multiplied the index by two, the remaining (iv, v) by one.

The index was normalised to range from 0 to 1. Thus our simple dispersal ability index has the following formula:

$$DI = ((100/\max_{SVL}) * SVL) * CI * Ad-Hab * EcoT * L-Hab).$$

3.4.2.3.3 Range size

In order to keep distributional bias at a minimum we did neither use estimated distribution polygons nor similar proxies (e.g. areas of occupancy, estimates of occurrence). Instead we extrapolated occurrence records with the aid of an ENM algorithm (Maxent) to infer a more

objective range sizes for each individual species. ENM is a statistical modelling technique and in our case contrasts environmental parameters from known occurrences against randomly created “pseudo-absences” by maximising entropy (Phillips *et al.* 2004, 2006; Phillips & Dudík 2008; Elith *et al.* 2011). The method is well suited when absences are unknown and when only low numbers of occurrences exist (Elith *et al.* 2006; Heikkinen *et al.* 2012). ENMs were calculated for the whole African continent, cut at the 10 percentile threshold and manually corrected for biogeographic barriers. The ENMs employed 18 environmental parameters on a 30 Arc second grid (see Penner *et al.* 2013 and app. 3.4.2-1, tab. 3.4.1-1 for details).

3.4.2.3.4 Niche breadth

We calculated niche breadth for the environmental niche only. First we run a spatial PCA of all 18 environmental parameters (see above; using ESRI ArcGIS 10.0). Afterwards we extracted the maximum, minimum and mean values as well as standard deviations for three PCA axes over the modelled range of all species.

3.4.2.3.5 Statistics

To test the correlations between dispersal, range sizes and niche breadths we calculated multiple Spearman-rank correlation tests with a Bonferroni correction (R software 3.0.1 (2013); ltm package, Rizopolous 2006). The categorical nature of our data set (see above) did not allow for any parametric tests.

3.4.2.4 Results

There was a highly significant correlation between mean niche breadth, measured as environmental variance throughout the range of a species, and range size [Spearman-rank correlation with Bonferroni correction for the first two PCA axes [see fig. 1; $p < 0.001$; $\rho = -0.608$ (PCA1); $p < 0.001$; $\rho = -0.581$ (PCA2)]. There was also a correlation between the variance of the environmental niche (standard deviation) and the range sizes for the third PCA axis [see fig. 1; $p < 0.001$; $\rho = 0.538$]. The explained variation was 87.1 % (PCA1), 11.9 % (PCA2) and 0.9 % (PCA3). The correlation between our dispersal ability index and range sizes was highly significant (Spearman-rank correlation, $p < 0.001$; $\rho = 0.505$; fig. 2).

3.4.2.5 Discussion

Herein, we showed that a simple dispersal measure can be used as an alternative explanation to the question why some species have larger range sizes than others. This contradicts a previous study investigating this link (Lester *et al.* 2007) and confirms the general notion that niche breadths are correlated with range sizes (Brown 1984, Slatyer *et al.* 2013).

3.4.2.5.1 Dispersal & range size

In general, a wide range of factors, spanning metabolic, time, risk and opportunity variables, make dispersal a costly task, either directly or indirectly (Bonte *et al.* 2012). Despite these costs and the fact that amphibians are considered poor dispersers due to a number of ecological factors (e.g. semipermeable skin leading to easy desiccation, habitat specificity), dispersal is important in amphibians (e.g. Funk *et al.* 2005 and reviews by Marsh & Trenham 2001, Smith & Green 2005) as for most other species. Nevertheless, dispersal abilities are highly variable between and within amphibian species, e.g. ranging from 2.5 to 15 km per year in *Rhinella marina* (Marsh & Trenham 2001) and more than 1 km in one night in *Hoplobatrachus occipitalis* (Spieler & Linsenmair 1998). Absolute distances of individuals are naturally much higher with a recorded maximum of 34 km by *Anaxyrus fowleri* (see review by Smith & Greene 2005). However, measuring dispersal abilities is not straightforward and a simple measure is desired to

circumvent the logistical problem to gather these data. We are not aware of an existing simple measure. Previous work concentrated on one method (radio-tracking, mark-recapture or genetic methods; see introduction) and did not aim at detecting universalities.

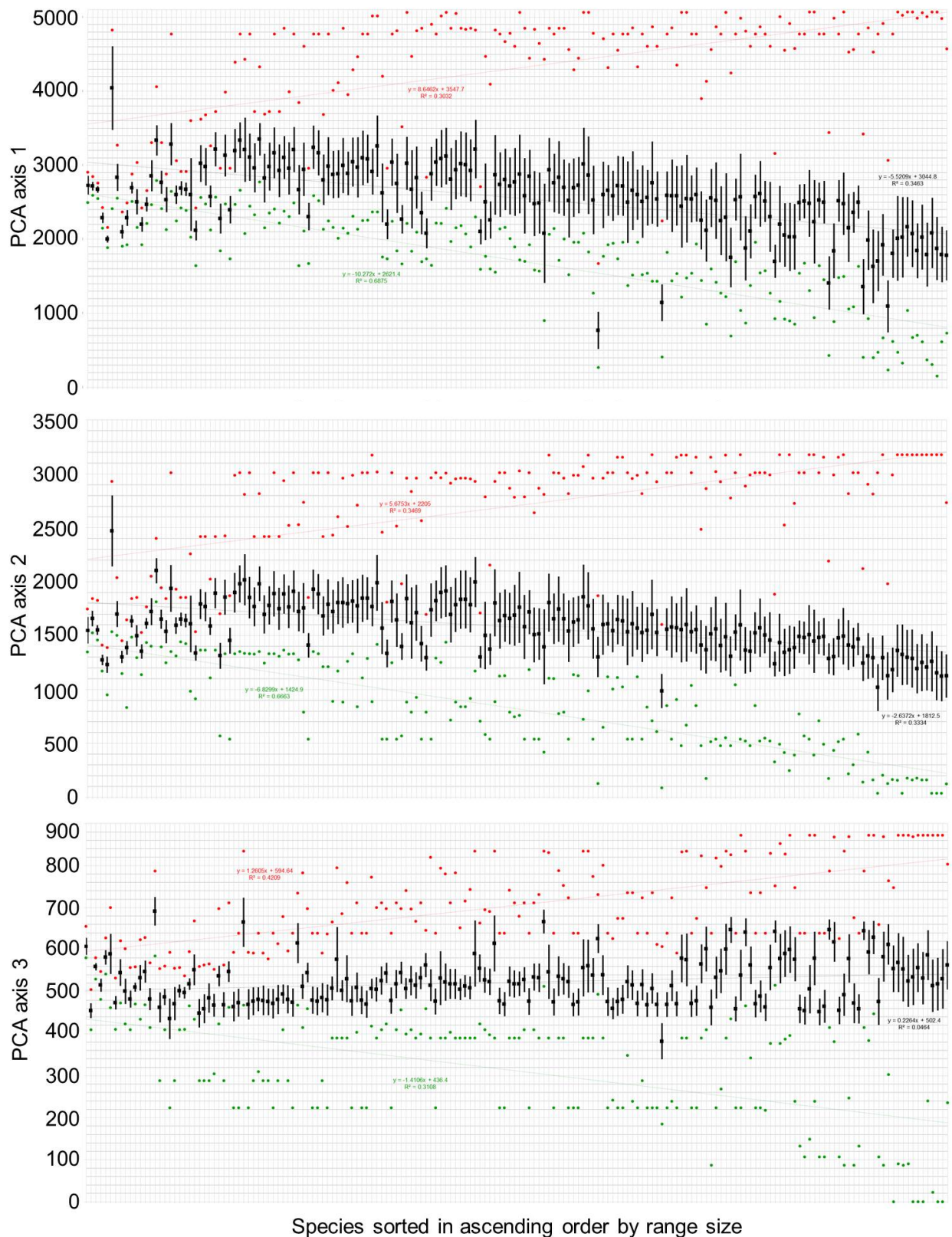


Fig. 3.4.1-2: Correlation between range sizes, derived from ENM, and the calculated dispersal ability index (Spearman-rank correlation, $p < 0.001$; $\rho = 0.496$), derived from body size and habitat information (see text) for all 176 West African amphibians analysed (see also S1 for details).

Similar to the studies on passerine birds (Laube *et al.* 2013), one might intuitively argue that the ratio between hind leg length (or femur length) and body length (or snout-vent length) might be a useful proxy. Certainly, frogs with longer hind legs can jump further and therefore cover long distances in a short period of time. However, it was also shown that leg muscles of jumping frogs fatigue faster than that of “walking” species (Renaud & Stevens 1983; Chadwell *et al.* 2002). Thus we looked for other variables which influence dispersal. The five niche characteristics (snout-vent-length, clutch size, habitats used by adults, ecotypes of adults and habitats used by larvae; see material and methods section for their justification) used in our dispersal ability index are relatively easy to obtain for other amphibian taxa as well as for other animal groups. Applying the dispersal ability index to other groups might need some slight but easy to conduct modifications, e.g. maybe replacing snout-vent length by body mass if snout-vent length is difficult to obtain, standardising clutch/litter size to reproductive output per defined time span if individual reproductive events do not take place every year. Thus, the index should be generally testable. In our case it permitted us to develop a measurement of dispersal for a group where observation data on dispersal is very scarce. So far for West African amphibians such data exists only for two species: *Hoplobatrachus occipitalis* and *Phrynobatrachus guineensis*; with completely different ecologies (*H. occipitalis*: large, aquatic, nearly ubiquitous, large range size vs. *P. guineensis*: small, terrestrial to arboreal, highly specialised, small range size). Furthermore, published dispersal data often is not comparable because of the highly different methods used, e.g. radio-tracking for *H. occipitalis* (Spieler & Linsenmair 1998) and analysis of microsatellites in *P. guineensis* (Sandberger *et al.* 2010). Our dispersal ability index confirmed the former results for both species, ranking *H. occipitalis* high (3rd place, out of 176) and *P. guineensis* last. Nevertheless, at least on a small scale (less than 1.5 km maximum distance between two populations) even the small (< 20 mm SVL), highly specialised (breeding only in tiny temporary water bodies, such as tree holes or water filled snail shells), leaf litter frogs *P. guineensis* seem to be highly mobile, revealing no apparent genetic structure (Sandberger *et al.* 2010).

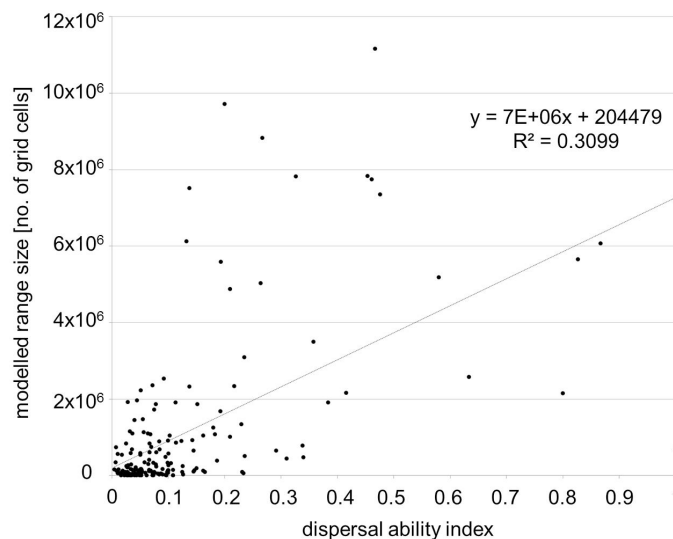


Fig. 3.4.2-1: Mean environmental niche breadth over the species range with variance (standard deviation), minima (green) and maxima (red). Niche breadth was measured as environmental variance, derived from a spatial PCA of 18 environmental parameters, throughout the whole range of a species. Shown are the values for three PCA axes for all 176 analysed West African amphibian species, sorted by their range size (25 to 111,533,90 grid cells of 30 Arc seconds which approximate 1 km²) in ascending order (see also S1 for details).

Our question, whether “good dispersing species do have a wide range” can be answered positively. In addition, our study also offers an alternative explanation for the sometimes assumed direct link between larger species and larger range sizes. Though this was not observed in our case (Sperman-rank correlation, $p > 0.999$; ρ (males) = 0.225; ρ (females) = 0.205), it was previously reported for anurans from Australia (Murray *et al.* 1998) and the Brazilian Cerrado (Olalla-Tárraga *et al.* 2009) as well as a large number of other taxa ranging from plants to mammals (see review by Gaston 2003).

3.4.2.5.2 Applications

The importance of our findings is twofold. First, it has implications for studies investigating the influence of climate change with the help of ENM. Currently, under different climate change scenarios and models, studies either assume no dispersal, unlimited dispersal or a previously defined limited dispersal distance. However, we suggest that a dispersal ability index can be used to adapt the dispersal limit of each species to each ENM run without having to measure its dispersal capabilities in the field. Another easier possibility would be to use the range size of a species as a proxy for its dispersal ability, thus adjusting the climate change ENMs individually for the range size of each species modelled.

Second, our work is important for conservation because it was already shown that a number of biological factors determine the susceptibility of amphibians to threats, though these factors were not detailed (Bielby *et al.* 2006). Thus, our results mean that amphibian species with small ranges do have low dispersal abilities, both factors contributing to their risk of extinction.





4 Discussion

4.1 General discussion

Questions of where species are distributed and why, have puzzled scientists for a long time and continue to do so (e.g. Lomolino *et al.* 2004). Despite numerous studies, especially in recent times with the emergence of ENM, the focus has mainly been on a global perspective or on parts of the Western world, employing rather coarse scales. Herewith, biogeographical and macroecological work conducted on a relatively large region - West Africa is presented.

A solid taxonomic base is of high importance for ecological studies. During the first part, three examples of taxonomic clarifications were shown. The so called Puddle frogs (family Phrynobatrachidae) currently contain 27 species in West Africa. The species are predominantly small species (approximately 12 to 40 mm snout-vent length) which mostly live on the ground and in the leaf litter. Two members of the family, *Phrynobatrachus liberiensis* and *P. plicatus*, which reach the upper size limit of the species, live only in forests of West Africa. *P. liberiensis* occurs throughout the western part of the Upper Guinea forests. *P. plicatus* has a very similar distribution often occurring in sympatry but ranges much further eastwards into Central Africa. Studies in south-western Ghana revealed a rather large *Phrynobatrachus* (approximately 23-28 mm) with close resemblance in morphological and colour pattern to *P. liberiensis* and *P. plicatus*. Due to its somehow intermediate but unique combination of characters as well as genetic differences (minimum 3.4%) to both species, the new species *Phrynobatrachus intermedius* was described (chapter 3.1.1).

The second example evaluated the taxonomic status of two described species of Reed frogs (family Hyperoliidae). *Hyperolius nitidulus* was described in 1875 by Peters and *Hyperolius spatzi* in 1931 by Ahl (chapter 3.1.2). However, many species of this family show highly variable colour patterns and a number of questionable taxa exist. *H. nitidulus* and *H. spatzi* are both, at first glance, similarly looking savannah species albeit described from different areas: *H. nitidulus* from south-western Nigeria and *H. spatzi* from eastern Senegal. Morphological, acoustic and genetic data exposed clear differences and confirmed both species without overlapping ranges: *H. spatzi* is restricted to Senegal and *H. nitidulus* ranges from Guinea to Central Africa.

In the third example, the Western Night frog, *Astylosternus occidentalis* (Arthroleptidae), is a well-known species living in the rain forest zone of Sierra Leone, Liberia and parts of adjacent Guinea. Specimens discovered in south-western Ghana and south-eastern Côte d'Ivoire clearly belonged to the genus but differed in morphological and genetic characters. Therefore, a new species, *Astylosternus laticephalus*, was described (chapter 3.1.3).

Despite a great deal of taxonomic work in West Africa by Mark-Oliver Rödel and his working group, certainly not all species have been discovered and are described yet. A number of candidate species (see Vieites *et al.* 2009) are work in progress of the working group. Moreover, the genus *Arthroleptis* is still in taxonomic disorder. So far, genetic and morphological analyses have not provided a solution. In addition, there exists a number of survey gaps in West Africa and it is highly likely that well over 200 amphibian species range throughout the region.

Looking at species distributions of the known taxa, one might get the impression that West Africa harbours many species which occur only in the West African region. However, the question whether it is really a unique region was never really tested for amphibians. In many biogeographical treatments West Africa is commonly seen as a subset of Central Africa (see chapter 3.2). Using data on amphibian assemblages across the whole African continent south of the Saharan desert, compositional similarities were compared with multivariate statistics. A consensus cluster out of 21 clusters was created, a new technique in ecology. This revealed that assemblages in West Africa were more similar to each other than to assemblages in Central Africa. These results were surprising because they grouped assemblages of the regions together despite the fact that they were located in very distinct habitats, ranging from forests to savannahs. Furthermore, a clear border was discovered which separated West from Central Africa, the Cross River, which is situated along the border between Nigeria and Cameroon. Subdivisions within West Africa were also detected and again rivers acted as main barriers. So

one might ask why the Cross River constitutes such a distinct border. Superficially it looks very similar to other rivers in West and Central Africa. However, paleontological models suggest that between 50 and 100 Ma ago a large bay of saltwater stretched far inland (Scotese 2001). This corresponds well with estimations when most African species evolved (see Moritz *et al.* 2000; Wieczorek *et al.* 2000; Zimkus *et al.* 2010 and references therein).

Although West African amphibians are unique, their threats are not. As in many other regions of the world, habitat alteration and destruction is the number one cause for the decline of many populations. Another major cause of amphibian population declines throughout the world is *Batrachochytrium dendrobatidis* (*Bd*). It is widespread in Africa and a fine grained continental model demonstrated a high environmental suitability in West Africa. However, although the sample size was large and different techniques and labs were used, no positive records were noted west of the Dahomey Gap (chapter 3.3). It represents a large natural gap in the forest belt in which savannahs stretch to the coast. As *Bd* is sensitive to hot and dry climate, the Dahomey Gap seems to form a natural barrier to the spread of *Bd* into West Africa. In order to keep the region *Bd* free, it is highly recommended to follow established protocols to disinfect equipment imported to the region.

Chapter 3.2 analysed amphibian assemblages throughout the continent. It is obvious that point data will always leave gaps between points where the presence of a species is unknown. Nevertheless, complete information on the precise occurrences over a large extent and on a fine resolution is urgently needed by conservation and political decision makers. As this is impossible to achieve with the aid of standard monitoring techniques, several modelling techniques exist to extrapolate from the known occurrences into the complete spatial area. ENM for West African amphibians was applied to gain a map of alpha diversity (chapter 3.4.1). The results show that it is possible to use binary maps derived from the ENMs but also the likelihoods from the ENMs. Furthermore, the data (alpha diversity as well as threatened, endemic and evolutionary distinct taxa) shows that in some areas the coverage of protected areas seem to work (e.g. south-western Ghana) and that in others there is a need for new protection measures (e.g. north-western Liberia). From a biogeographical point of view the hotspot “Guinean forests of West Africa” (Myers *et al.* 2000) and the WWF ecoregions (Olson *et al.* 2001) are in some areas confirmed (e.g. eastern parts of the Upper Guinea forests) but not in others (e.g. Fouta Djallon) and therefore highlight the importance of fine scale approaches. From a methodological point of view, the choice of diversity measure is not as important as the difference between the use and respectively the non-use of spatial filtering. The latter greatly distorts the overall results.

A recent meta-analysis across many animal and plant taxa supported the hypothesis that niche breadth can explain species range sizes. However, as described in chapter 3.4.2, the niche is quite a complex concept and it might be possible to use only parts of the niche to explain the observed pattern. While chapter 3.4.1 calculated the environmental niche of West African amphibians, there are many more aspects of a niche which were not included. Using basic species traits, a simple measure of dispersal ability was calculated. Despite the fact that niche breadth, calculated from the environmental niche only, explained range sizes, dispersal ability was able to explain range sizes as well. This finding could potentially help when modelling the distributions of species under different future global change scenarios and models. Up to now these ENMs, run under global change models, assume either no dispersal, full dispersal or a priori set dispersal limits. The results from chapter 3.4.2 suggest to use the presented dispersal ability index (or range size as a proxy) to achieve more realistic distribution models.

4.2 Outlook

The presented work fills an important gap for West Africa but also on a global perspective. Besides providing data for amphibian conservation, several methodological aspects could advance macroecological research. The following three fields are briefly highlighted.

First, in the presented approach testing the coverage of the modelled biodiversity by existing protected areas, it is assumed that all protected areas are equally protected. Further steps

should include information on the legal as well as real status of the areas and could apply algorithms which identify the most important areas with respect to a priori selected criteria. A number of such algorithms exist (e.g. Moilanen *et al.* 2005; Moilanen 2007; Ball *et al.* 2009) but up to date have not been compared extensively. Thus no general “best practice guidelines” have been established yet. Potentially, these algorithms could pinpoint single protected areas and that way emphasise even more to decision makers where conservation priorities have to be set. Unfortunately, the governments of the West African countries have not committed themselves to a regional conservation plan despite the fact that the majority of natural habitats are already destroyed (Mayaux *et al.* 2005, 2013). Nevertheless, a realistic chance for biodiversity in general and amphibian diversity in particular can only be achieved if the majority of countries act in concert.

Second, so far the ENMs were used to calculate alpha diversity. From a biogeographical point of view it is also important to identify the areas where “species turnover” (beta diversity) takes place. This will further identify coherent areas and barriers and supplement the analysis presented in chapter 3.2. However, the field of calculating beta diversity is very diverse and recent attempts have just started to clarify some terminological and methodological issues (e.g. see Tuomisto 2010a, b). Very few attempts have been conducted using raster data (e.g. McKnight *et al.* 2007) and therefore several methodological problems remain unanswered. Furthermore, due to the extent and fine resolution of the presented study area (2760 by 4800 grid cells), it is impossible to calculate beta diversity on a standard computer with standard software. These logistical (hardware and software) problems need to be tackled in the future. The additional information of phylogenetic and functional diversity in ENM approaches would allow the pursuit of more integrative questions and put the analyses in a broader context. However, complete data sets, even for the 176 species analysed with the ENMs, are not available yet.

Third, global change will also affect West Africa. A variety of scenarios and models exist and there are large agreements as well as disagreements between them (see IPCC 2013). The current commonly used approach calculates so called ensemble models. Nevertheless, they are mostly based on a global view but data basis for West Africa is quite scarce (see Hijmans *et al.* 2005 for current data and Willis *et al.* 2013 for past data which should be used to calibrate future models). In addition, the current approaches only include information on climate but neglect potential changes in land cover. Future analyses on an ensemble basis and incorporating land cover information will show how global change might influence amphibians in West Africa, how regional models can be compared against the global scale, and whether they can enhance our understanding of potential global change impacts.





5 Acknowledgements

I am deeply grateful to Mark-Oliver Rödel for introducing me to the scientific herpetological world and offering me the job within the BIOTA project as well as the possibility to conduct a PhD. Without him and his long lasting support the thesis would never have been achieved. I am thankful and happy that I was always allowed to follow his and at the same time my own path! The department Zoology 3 at the University of Würzburg provided a great starting point for the thesis and the Museum für Naturkunde continued along that line.

Within the framework of the BIOTA project, the ENM parameters were provided by Jakob Fahr, Matthias Herkt, Günther Barnickel and Martin Wegmann. Their help is highly appreciated. It would have taken much longer without them.

The German Ministry for Education and Research (BMBF) was generous in funding the BIOTA-West project (funding number 01LC0617J). My gratitude also includes the BIOTA coordination team K. Eduard Linsenmair and Minnatallah Boutros as well as all the responsible governments, their ministries for issuing permits and the numerous field assistants who provided invaluable help during field trips of my own or by colleagues who allowed me to use their data. The Future SOC Lab of the Hasso-Plattner-institute kindly granted access to their computer hardware, facilitating alpha diversity calculations a lot. In addition, I am much obliged to the EU BON project, especially Christoph Häuser and Anke Hoffmann in always giving me the freedom needed to do the splits between the thesis, that project and my other duties.

A number of people helped by gathering, digitising data or by generously providing their own data! There are too many to mention. My sincere thanks to you and all your hard work involved and especially to Michael F. Barej, Caleb Ofori-Boateng, Christian Brede, Matthias Dahmen, Nono LeGrand Gonwouo, Franziska Grözinger, Annika Hillers, Mareike Hirschfeld, N'Goran Kouamé, Jenja Kronenbitter, Meike Mohnke, Joachim Nopper, Mark-Oliver Rödel and Anja Wetzel!

I would also especially like to acknowledge the sensational support by Moritz Augustin. He provided invaluable advice, discussion, mathematical knowledge and programming skills!

Furthermore, I would like to thank all the members of herpetology working group for their support, discussions, help, chocolate, cookies and beer. Office mates are of unmeasurable importance, without them one could go crazy with all the research and its associated hurdles. My special thanks to Tillmann Konrad as well as to Michael F. Barej, Mirjana Bevanda, Sanja Drakulic, Franziska Grözinger, Annika Hillers, Mareike Hirschfeld, Meike Mohnke, Laura Sandberger and Nadine Zacharias, including all others with whom I worked. A major stress reliever component was sports. Thanks a lot to all involved, especially to the hockey teams of the HTC Würzburg and the Berliner SC!

Moral support was generously provided throughout all this time by Martin (Oggi) Wegmann. The help and assistance of Petra Kube, Tillmann Konrad, my parents and family cannot be put into appropriate words. They would all fall too short. I owe them more than a lot! Thank you!

Finally, the biggest thanks go to Petra and Helena. They remind me every day, why I am doing what I am doing and that it is worth it! All this despite the fact that I am often doing weird things, which they have to cope with, such as trips to remote places in Africa and work in projects at the university and the museum besides working on the thesis... Thank you, I love you!





6 Bibliography

- Aanensen DM (2011) *Bd-Maps*. www.bd-maps.net (last accessed 28 February 2012).
- Achard F, Eva HD, Stibig H-J, Mayaux P, Gallego J, Richards T & Malingreau J-P (2002) Determination of deforestation rates of the world's humid tropical forests. *Science* 297: 999-1002.
- Adams MJ, Chelgren ND, Reinitz D, Cole RA, Rachowicz LJ, Galvan S, McCreary B, Pearl CA, Bailey LL, Bettaso J, Bull, EL & Leu M (2010) Using occupancy models to understand the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecological Applications* 20: 289-302.
- Adeba PJ, Kouassi P & Rödel M-O (2010) Anuran amphibians in a rapidly changing environment - revisiting Lamto, Côte d'Ivoire, 40 years after the first herpetofaunal investigations. *African Journal of Herpetology* 59: 1-16.
- Adum GB, Eichhorn MP, Oduro W, Ofori-Boateng C & Rödel M-O (2013) Two-stage recovery of amphibian assemblages following selective logging of tropical forests. *Conservation Biology* 27: 354-363.
- Ahl E (1931a) Zur Systematik der afrikanischen Arten der Baumfroschgattung *Hyperolius* (Amph. Anur.). *Mitteilungen aus dem zoologischen Museum Berlin* 17: 1-132.
- Ahl E (1931b) Anura III, Polypedatidae. In: Schulze FE & Kükenthal W (eds) *Das Tierreich* 55. Lieferung. Walter de Gruyter, Berlin & Leipzig, Germany. I-XVI + 1-477.
- Aide TM & Rivera E (1998) Geographic patterns of genetic diversity in *Poulsenia armata* (Moraceae): implications for the theory of Pleistocene refugia and the importance of riparian forest. *Journal of Biogeography* 25: 695-705.
- Akani GC, Politano E & Luiselli L (2004) Amphibians recorded in forest swamp areas of the River Niger Delta (southeastern Nigeria), and the effects of habitat alteration from oil industry development on species richness and diversity. *Applied Herpetology* 2: 1-22.
- Altig R & McDiarmid RW (1999) Diversity: familial and generic characterizations. In: McDiarmid RW & Altig R (eds.) *Tadpoles: The biology of anuran larvae*. University of Chicago Press, Chicago, USA. 295-337.
- Amiet J-L (1971) Le têtard d'*Astylosternus corrugatus* Boulenger (Amphibien Anoures). *Annales de la Faculté des Sciences du Cameroun* 6: 85-98.
- Amiet J-L (1973) Compte rendu d'une mission batrachologique dans le Nord-Cameroun. *Annales de la Faculté des Sciences du Cameroun* 12: 63-78.
- Amiet J-L (1975) Ecologie et distribution des amphibiens anoures de la région de Nkongsamba (Cameroun). *Annales de la Faculté des Sciences de Yaoundé* 20: 33-107.
- Amiet J-L (1977) Les *Astylosternus* du Cameroun (Amphibia Anura, Astylosterninae). *Annales de la Faculté des Sciences de Yaoundé* 23-24: 99-227.
- Amiet J-L (1987) Aires disjointes et taxons vicariants chez les anoures du Cameroun: implications paléoclimatiques. *Alytes* 6: 99-115.
- Amiet J-L (1989) Quelques aspects de la biologie des amphibiens anoures du Cameroun. *Année Biologique* 28: 73-136.
- Andersson LG (1937) Reptiles and batrachians. Collected in the Gambia by Gustav Svensson and Birger Rudebeck (Swedish Expedition 1931). *Arkiv för zoologi* 29A: 1-28.
- Angel F (1930) Sur les têtards d'un batracien anoure d'Afrique, de la famille des ranidés (groupe des astylosterninés). *Bulletin de la Société zoologique de France* 55: 219-222.
- Angel F (1944) Une nouvelle espèce d'Amphibien (genre *Hylambates* de la Haute-Guinée française) Matériaux de la Mission Lamotte au Mont Nimba en 1942. *Bulletin du Muséum national d'Histoire Naturelle, Ser. 2* 16: 420-421.
- Annis SL, Dastoor FP, Ziel H, Daszak P & Longcore JE (2004) A DNA-based assay identifies *Batrachochytrium dendrobatidis* in amphibians. *Journal of Wildlife Diseases* 40: 420-428.
- Anthony NM, Johnson-Bawe M, Jeffery K, Clifford SL, Abernethy KA, Tutin CE, Lahm SA, White LJT, Utey JF, Wickings EJ & Bruford MW (2007) The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. *Proceedings of the National Academy of Sciences* 104: 20432-20436.
- Araujo MB, Thuiller W & Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712-1728.
- Arnaud M & Leroy M (1991) SPOT 4: a new generation of SPOT satellites. *ISPRS Journal of Photogrammetry and Remote Sensing* 46: 205-215.
- Assemian NE, Kouamé NG, Tohé B, Gourène G & Rödel M-O (2006) The anurans of the Banco National Park, Côte d'Ivoire, a threatened West African rainforest. *Salamandra* 42: 41-51.
- Auckland LC (1997) The effect of selective logging on amphibian diversity of Budongo Forest, Uganda. Undergraduate honours project, University of Oxford, Oxford.



- Austin JD, Dávila JA, Lougheed SC & Boag PT (2003) Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology* 12: 3165-3172.
- Baard EHW & de Villiers AL (2000) State of biodiversity: Western Cape Province, South Africa. *Amphibians and reptiles. Western Cape Nature Conservation Board, South Africa.* 1-31.
- Bai C, Liu X, Fisher MC, Garner TWJ & Li Y (2012) Global and endemic Asian lineages of the emerging pathogenic fungus *Batrachochytrium dendrobatidis* widely infect amphibians in China. *Diversity and Distributions* 18: 307-318.
- Bakarr, M., Bailey, B., Byler, D., Ham, R., Olivieri, S. & Omland, M. (2001) From the forest to the sea: biodiversity connections from Guinea to Togo, Conservation Priority-Setting Workshop, December 1999. Conservation International, Washington DC, USA. 1-78.
- Baláz V, Kopecký O & Gvoždík V (2012) Presence of the amphibian chytrid pathogen confirmed in Cameroon. *Herpetological Journal* 22: 191-194.
- Balinsky BI (1962) Patterns of animal distribution on the African continent. *Annals of the Cape Provincial Museums* 2: 299-310.
- Ball IR, Possingham HP & Watts M (2009) Marxan and relatives: Software for spatial conservation prioritisation. Chapter 14. In: Moilanen A, KA Wilson & Possingham HP (eds) *Spatial conservation prioritisation: Quantitative methods and computational tools*. Oxford University Press, Oxford, UK. 185-195.
- Bancroft BA, Han BA, Searle CL, Biga LM, Olson DH, Kats LB, Lawler JJ & Blaustein AR (2011) Species level correlates of susceptibility to the pathogenic amphibian fungus *Batrachochytrium dendrobatidis* in the United States. *Biodiversity and Conservation* 20: 1911-1920.
- Barbault R (1967) Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): Le cycle annuel de la biomasse des amphibiens et des lézards. *Terre Vie* 3: 297-318.
- Barbault R (1972) Les peuplements d'amphibiens des savanes de Lamto (Côte d'Ivoire). *Annales de l'Université d'Abidjan Sér. E* 5: 59-142.
- Barej MF, Böhme W, Perry SF, Wagner P & Schmitz A (2010) The hairy frog, a curly fighter? - A novel hypothesis on the function of hairs and claw-like terminal phalanges, including their biological and systematic significance (Anura: Arthroleptidae: *Trichobatrachus*). *Revue Suisse de Zoologie* 117: 243-263.
- Barej MF, Rödel M-O, Gonwouo LN, Pauwels OSG, Böhme W & Schmitz A (2010) Review of the genus *Petropedetes* Reichenow, 1874 in Central Africa with the description of three new species (Amphibia: Anura: Petropedetidae). *Zootaxa* 2340: 1-49.
- Barnett K L, Emms C & Santoni C (2001) The herpetofauna of Abuko Nature Reserve, The Gambia. *Herpetological Bulletin* 77: 5-14.
- Barnett LK & Emms C (2005) Common amphibians of the Gambia. Makasutu Wildlife Trust, Serrekunda, The Gambia. 1-24.
- Barthlott W, Mutke J, Rafiqpoor D, Kier G & Kreft H (2005) Global centers of vascular plant diversity. *Nova Acta Leopoldina* 342: 61-83.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology & Biogeography* 19: 134-143.
- Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology & Biogeography* 21: 1223-1232.
- Beck CW & Congdon JD (2000) Effects of age and size at metamorphosis on performance and metabolic rates of southern toad, *Bufo terrestris*, metamorphs. *Functional Ecology* 14: 32-38.
- Becker CG & Zamudio KR (2011) Tropical amphibian populations experience higher disease risk in natural habitats. *Proceedings of the National Academy of Sciences* 108: 9893-9898.
- Behangana M & Arusi J (2004) The distribution and diversity of amphibian fauna of Lake Nabugabo and surrounding areas. *African Journal of Ecology* 42: 6-13.
- Behangana M (2004) The diversity and status of amphibians and reptiles in the Kyoga Lake Basin. *African Journal of Ecology* 42: 51-56.
- Bell RC, Garcia AVG, Stuart BL & Zamudio KR (2011) High prevalence of the amphibian chytrid pathogen in Gabon. *EcoHealth* 8: 116-120.
- Berger L & Parker JM (1999) In: Speare R & Berger L. (2000) Global distribution of chytridiomycosis in amphibians. <http://www.jcu.edu.au/school/phtm/PHTM/frogs/chyglob.htm> (last accessed: 26 April 2011).
- Berger L, Speare R & Kent A (1999). Diagnosis of chytridiomycosis in amphibians by histologic examination. *Zoo's Print Journal* 15: 184-190.



- Berger L, Speare R & Kent A (2001) Diagnosis of chytridiomycosis in amphibians by histologic examination. In: Speare R & Steering Committee of Getting the Jump on Amphibian Disease (eds) Developing management strategies to control amphibian diseases: Decreasing the risks due to communicable diseases. Townsville, School of Public Health and Tropical Medicine, James Cook University, Australia. 83-93.
- Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL, Slocumbe R, Ragan MA, Hyatt AD, McDonald KR, Hines HB, Lips KR, Marantelli G & Parkes H (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences* 95: 9031-9036.
- Berger L, Speare R, Hines HB, Marantelli G, Hyatt AD, McDonald KR, Skerratt LF, Olsen V, Clarke JM, Gillespie G, Mahony M, Sheppard N, Williams C & Tyler MJ (2004) Effect of season and temperature on mortality in amphibians due to chytridiomycosis. *Australian Veterinary Journal* 82: 31-36.
- Berger L, Speare R, Hyatt AD (1999) Chytrid fungi and amphibian declines: overview, implications and future directions. In: Campbell, A, editor. *Declines and disappearances of Australian frogs*. Canberra, Environment Australia. pp. 23-33.
- Berven KA & Grudzien TA (1990) Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44: 2047-2056.
- Bielby J, Cunningham AA & Purvis A (2006) Taxonomic selectivity in amphibians: ignorance, geography or biology? *Animal Conservation* 9: 135-143.
- Blach-Overgaard A, Svenning J-C, Dransfield J, Greve M & Balslev H (2010) Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33: 380-291.
- Blackburn DC & Wake DB (2011) Class Amphibia Gray, 1825. In: Zhang Z-Q (ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 39-55.
- Blackburn DC, Gonwouo LN, Ernst R & Rödel M-O (2009) A new squeaker frog (Arthroleptidae: *Arthroleptis*) from the Cameroon volcanic line with redescription of *Arthroleptis frederici* Nieden, 1911 "1911" and *A. variabilis* Matschie, 1893. *Breviora* 515: 1-22.
- Blackburn DC, Hanken J & Jenkins FA (2008) Concealed weapons: erectile claws in African frogs. *Biology Letters* 4: 355-357.
- Blaustein AR, Wake DB & Sousa WP (1994) Amphibian declines: Judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8: 60-71.
- Boettger O (1881) Aufzählung der von Frhrn. H. und Frfr. A. von Maltzahn im Winter 1880/81 am Cap Verde in Senegambien gesammelten Kriechtiere. *Abhandlungen Senckenbergisch naturforschenden Gesellschaft Frankfurt a.M.* 12: 393-419 + 1 plate.
- Böhm M, Collen B, Baillie JEM, Bowles P, Chanson J, Cox N, Hammerson G, Hoffmann M, Livingstone SR, Rama M, Rhodin AGJ, Stuart SN, van Dijk PP, Young BE, Afuang LE, Aghasyan A, García A, Aguilar C, Ajtic R, Akarsu F, Alencar LRV, Allison A, Ananjeva N, Anderson S, Andrén C, Ariano-Sánchez D, Arredondo JC, Auliya M, Austin CC, Avci A, Baker PJ, Barreto-Lima AF, Barrio-Amorós CL, Basu D, Bates MF, Batistella A, Bauer A, Bennett D, Böhme W, Broadley D, Brown R, Burgess J, Captain A, Carreira S, del Rosario Castañeda M, Castro F, Catenazzi A, Cedeño-Vázquez JR, Chapple DG, Cheylan M, Cisneros-Heredia DF, Cogalniceanu D, Cogger H, Corti C, Costa GC, Couper PJ, Courtney T, Crnobrnja-Isailovic J, Crochet P-A, Crother B, Cruz F, Daltry JC, Daniels RJR, Das I, de Silva A, Diesmos AC, Dirksen L, Doan TM, Dodd Jr CK, Doody JS, Dorcas ME, Duarte de Barros Filho J, Egan VT, El Mouden EH, Embert D, Espinoza RE, Fallabrino A, Feng X, Feng Z-J, Fitzgerald L, Flores-Villela O, França FGR, Frost D, Gadsden H, Gamble T, Ganesh SR, Garcia MA, García-Pérez JE, Gatus J, Gaulke M, Geniez P, Georges A, Gerlach J, Goldberg S, Gonzalez J-CT, Gower DJ, Grant T, Greenbaum E, Grieco C, Guo P, Hamilton AM, Hare K, Hedges SB, Heideman N, Hilton-Taylor C, Hitchmough R, Hollingsworth B, Hutchinson M, Ineich I, Iverson J, Jaksic FM, Jenkins R, Joger U, Jose R, Kaska Y, Kaya U, Keogh JS, Köhler G, Kuchling G, Kumlatas Y, Kwet A, La Marca E, Lamar W, Lane A, Lardner B, Latta C, Latta G, Lau M, Lavin P, Lawson D, LeBreton M, Lehr E, Limpus D, Lipczynski N, Lobo AS, López-Luna MA, Luiselli L, Lukoschek V, Lundberg M, Lymberakis P, Macey R, Magnusson WE, Mahler DL, Malhotra A, Mariaux J, Maritz B, Marques OAV, Márquez R, Martins M, Masterson G, Mateo JA, Mathew R, Mathews N, Mayer G, McCranie JR, Measey GJ, Mendoza-Quijano F, Menegon M, Métrailler S, Milton DA, Montgomery C, Morato SAA, Mott T, Muñoz-Alonso A, Murphy J, Nguyen TQ, Nilson G, Nogueira C, Núñez H, Orlov N, Ota H, Ottenwalder J, Papenfuss T, Pasachnik S, Passos P, Pauwels OSG, Pérez-Buitrago N, Pérez-Mellado V, Pianka ER, Pleguezuelos J, Pollock C, Ponce-Campos P, Powell R, Pupin F, Quintero Díaz GE, Radder R, Ramer J, Rasmussen AR, Raxworthy C, Reynolds R, Richman N, Rico EL, Riservato E, Rivas G, Rocha PLB da, Rödel M-O, Rodríguez Schettino L, Roosenburg WM, Ross JP, Sadek R, Sanders K, Santos-Barrera G, Schleich HH, Schmidt BR, Schmitz A, Sharifi M, Shea G, Shi H-T, Shine R, Sindaco R, Slimani T, Somaweera R, Spawls S, Stafford P, Stuebing R, Sweet S, Sy E, Temple HJ, Tognelli MF, Tolley K, Tolson PJ, Tuniyev B, Tuniyev S, Üzümae N, van Buurt G, Van Sluys M, Velasco A, Vences M, Veselý M, Vinke S, Vinke T, Vogel G, Vogrin M, Vogt RC, Wearn OR, Werner YL, Whiting MJ, Wiewandt T, Wilkinson J, Wilson B, Wren S, Zamin T, Zhou K, Zug G (2013) The conservation status of the world's reptiles *Biological Conservation* 157: 372-385.
- Böhme W & Nikolaus G (1989) Herpetological specimens from the Gotel Mountains and Mambilla Plateau, Nigeria. *Tauraco Research Report* 1: 28-30.



- Böhme W & Schneider B (1987) Zur Herpetofaunistik Kameruns (III) mit Beschreibung einer neuen *Cardioglossa* (Anura: Arthroleptidae). *Bonner zoologische Beiträge* 38: 241-263.
- Böhme W (1978) Zur Herpetofaunistik des Senegal. *Bonner zoologische Beiträge* 29: 360-417.
- Böhme W (1994) Frösche und Skinke aus dem Regenwaldgebiet Südost-Guineas, Westafrika. I. Einleitung; Pipidae, Arthroleptidae, Bufonidae. *herpetofauna* 16: 11-19.
- Bongers F, Poorter L, & Hawthorne WD (2004) The forests of Upper Guinea: gradients in large species composition. In: Poorter L, Bongers F, Kouamé FN & Hawthorne WD (eds) *Biodiversity of West African forests - An ecological atlas of woody plant species*. CABI Publishing, Oxford, UK. 41-52.
- Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Kustin K, Saastamoinen M, Schtickzelle N, Stevens VM, Vandewoestijne S, Baguette M, Barton K, Benton TG, Chaput-Bardy A, Clobert J, Dytham C, Hovestadt T, Meier CM, Palmer SCF, Turlure C & Travis MJM (2012). Costs of dispersal. *Biological Reviews* 87: 290-312.
- Bosch J, Carrascal LM, Duran L, Walker S & Fisher MC (2007) Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain; is there a link? *Proceedings of the Royal Society B* 274: 253-260.
- Bosch J, Martínez-Solano I & García-París M (2001) Evidence of a chytrid fungus infection involved in the decline of the common midwife toad (*Alytes obstetricans*) in protected areas of central Spain. *Biological Conservation* 97: 331-337.
- Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET, Grantham H, Kark S, Linke S, McDonald-Madden E, Pressey RL, Walker S, Wilson KA & Possingham HP (2008) Is conservation triage just smart decision making? *Trends in Ecology and Evolution* 23: 649-654.
- Boulenger GA (1882) *Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum*. 2nd ed. British Museum, London, UK. 1-503.
- Bourgat R (1979) Trématodes d'Amphibiens du Togo. *Bulletin du Muséum d'Histoire naturelle* 3: 597-624.
- Boyle DG, Boyle DB, Olsen V, Morgan JAT & Hyatt AD (2004) Rapid quantitative detection of chytridiomycosis (*Batrachochytrium dendrobatidis*) in amphibian samples using real-time Taqman PCR assay. *Diseases of Aquatic Organisms* 60: 141-148.
- Bradley GA, Rosen PC, Sredl MJ, Jones TR & Longcore JE (2002) Chytridiomycosis in native Arizona frogs. *Journal of Wildlife Diseases* 38: 206-212.
- Breden F (1987) The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* 1987: 386-395.
- Briggs CJ, Knapp RA & Vredenburg VT (2010) Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *Proceedings of the National Academy of Sciences* 107: 9695-9700.
- Broadley DG (1991) The Herpetofauna of northern Mwinilunga District, northwestern Zambia. *Arnoldia, Zimbabwe* 9: 51-538.
- Brooks TM, Balmford A, Burgess N, Fjeldså J, Hansen LA, Moore J, Rahbek C & Williams P (2001) Toward a blueprint for conservation in Africa. *BioScience* 51: 613-624.
- Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgri JD & Rodrigues ASL (2006) Global biodiversity conservation priorities. *Science* 313: 58-61.
- Brown JH & Maurer BA (1989) Macroecology: The division of food and space among species on continents. *Science* 243: 1145-1150.
- Brown JH (1984) On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255-279.
- Brown JH (1995) *Macroecology*. The University of Chicago Press, Chicago, USA. 1-269.
- Buckley LB & Jetz W (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal society B* 274: 1167-1173.
- Burger M, Branch WR & Channing A (2004) Amphibians and Reptiles of Monts Doudou, Gabon: Species turnover along an elevational gradient. In: Fisher BL (ed) *A floral and faunal inventory of Monts Doudou, Gabon, with reference to elevational distribution*. California Academy of Sciences Memoir 28, San Francisco, USA. 145-186.
- Burger M, Pauwels OSG, Branch WR, Tobi E, Yoga J-A & Mikolo E-N (2006) An assessment of the amphibian fauna of the Gamba Complex of Protected Areas, Gabon. *Gamba, Gabon: biodiversité d'une forêt équatoriale africaine / Gamba, Gabon: biodiversity of an equatorial African rainforest*. In: Alonso A, Lee ME, Campbell P, Pauwels OSG & Dallmeier F (eds). *Bulletin of the Biological Society of Washington* 12: 297-308.
- Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM, Kilahama FB, Loader SP, Lovett JC, Mbilinyi B, Menegon M, Moyer DC, Nashanda E, Perkin A, Rovero F, Stanley WT, Stuart SN (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* 134: 209-231.



- Burgess ND, D'Amico Hales J, Underwood E & Dinerstein E (2004) Terrestrial ecoregions of Africa and Madagascar - a conservation assessment. Island Press, Washington, DC, USA. 1-501.
- Burgin S, Schell CB & Briggs C (2005) Is *Batrachochytrium dendrobatidis* really the proximate cause of frog decline? *Acta Zoologica Sinica* 51: 344-348.
- Burrowes PA, Alicea A, Longo AV & Joglar RL (2011) Toes versus swabs? Evaluation of the best tissue source for detection of *Batrachochytrium dendrobatidis* in field-caught amphibians. *Herpetological Review* 42: 359-362.
- Bush AM, Markey MJ & Marshall CR (2004) Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. *Paleobiology* 30: 666-686.
- Cabrera-Guzmán E & Reynoso VH (2012) Amphibian and reptile communities of rainforest fragments: minimum patch size to support high richness and abundance. *Biodiversity and Conservation* 21: 3243-3265.
- Campbell A, Kapos V, Scharlemann JPW, Bubbs P, Chenery A, Coad L, Dickson B, Doswald N, Khan MSI, Hershaw F & Rashid M (2009) Review of the literature on the links between biodiversity and climate change: impacts, adaptation and mitigation. Secretariat of the Convention on Biological Diversity, Montreal, Technical Series No. 42: 1-124.
- Carey C & Alexander MA (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9: 111-121.
- Carey C, Bruzgul JE, Livo LJ, Walling ML, Kuehl KA, Dixon BF, Pessier AP, Alford RA & Rogers KB (2006) Experimental exposures of boreal toads (*Bufo boreas*) to a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*). *EcoHealth* 3: 5-21.
- Carey C, Dudley N & Stolton S (2000) Squandering paradise? The importance and vulnerability of the world's protected areas. WWF-World Wide Fund for Nature International, Gland, Switzerland. 1-232.
- Carwardine J, Wilson KA, Watts M, Etter A, Klein CJ & Possingham HP (2008) Avoiding costly conservation mistakes: the importance of defining actions and costs in spatial priority setting. *PLoS ONE* 3: e2586.
- Catenazzi A, Vredenburg VT & Lehr E (2010) *Batrachochytrium dendrobatidis* in the live frog trade of *Telmatobius* (Anura: Ceratophryidae) in the tropical Andes. *Diseases of Aquatic Organisms* 92: 187-191.
- Cayuela L, Golicher JD, Newton AC, Kolb M, Albuquerque FS, Arets EJMM, Alkemade JRM & Pérez AM (2009) Species distribution modelling in the tropics: problems, potentialities, and the role of biological data for effective species conservation. *Tropical Conservation Science* 2: 319-352.
- CBD (2013) Convention on Biological Diversity. <http://www.cbd.int> (last accessed 13 December 2013).
- Chadwell BA, Hartwell HJ & Peters SE (2002) Comparison of isometric contractile properties in hindlimb extensor muscles of the frogs *Rana pipiens* and *Bufo marinus*: Functional correlations with differences in hopping performance. *Journal of Morphology* 251: 309-322.
- Channing A, Finlow-Bates KS, Haarklau SE & Hawkes PG (2006) The biology and recent history of the critically endangered Kihansi Spray Toad *Nectophrynoides asperginis* in Tanzania. *Journal of East African Natural History* 95: 117-138.
- Channing A, Sinclair ARE, Mduma SAR, Moyer D, & Kreulen DA (2004) Serengeti amphibians: distribution and monitoring baseline. *African Journal of Herpetology* 53: 163-181.
- Chao A, Chiu C-H & Hsieh TC (2012) Proposing a resolution to debates on diversity partitioning. *Ecology* 93: 2037-2051.
- Chapman CA (1983) Speciation of tropical rainforest primates of Africa: insular biogeography. *African Journal of Ecology* 21: 297-308.
- Chase JM & Leibold MA (2003) Ecological niches, linking classical and contemporary approaches. The University of Chicago Press, Chicago, USA. 1-212.
- Chatelain C, Dao H, Gautier L, Spichiger R (2004) Forest cover changes in Côte d'Ivoire and Upper Guinea. In: Poorter L, Bongers F, Kouamé FN & Hawthorne WD (eds) *Biodiversity of West African forests - An ecological atlas of woody plant species*. CABI Publishing, Oxford, UK. 15-32.
- Chatelain C, Gautier L & Spichiger R (1996) A recent history of forest fragmentation in southwestern Ivory Coast. *Biodiversity and Conservation* 5: 37-53.
- Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution & Systematics* 6: 51-71.
- Chelgren ND, Pearl CA, Adams MJ & Bowerman J (2008) Demography and movement in a relocated population of Oregon spotted frogs (*Rana pretiosa*) - Influence of season and gender: *Copeia* 2008: 742-751.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143.



- Collen B, Ram M, Zamin T & McRae L (2008) The tropical biodiversity data gap: addressing disparity in global monitoring. *Tropical Conservation Science* 1:75-88.
- Collen B, Turvey ST, Waterman C, Meredith HMR, Kuhn TS Baillie JEM & Isaac NJB (2011) Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Philosophical Transactions of the Royal Society B* 366: 2611-2622.
- Colyn M, GautierHion A & Verheyen W (1991) A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography* 18: 403-407.
- Colyn M, Hulselmans J, Sonet G, Oudé P, De Winter J, Natta A, Nagy ZT & Verheyen E (2010) Discovery of a new duiker species (Bovidae: Cephalophinae) from the Dahomey Gap, West Africa. *Zootaxa* 2637: 1-30.
- Conradie W, Harvey J, Kotze A, Dalton DL & Cunningham MJ (2011) Confirmed amphibian chytrid in Mount Mulanje Area, Malawi. *Herpetological Review* 42: 369-371.
- Conradie W, Weldon C, Smith KG & du Preez LH (2011) Seasonal pattern of chytridiomycosis in common river frog (*Amietia angolensis*) tadpoles in the South African Grassland Biome. *African Zoology* 46: 95-102.
- Corn PS (2005) Climate change and amphibians. *Animal Biodiversity and Conservation* 28.1: 59-67.
- Crawford AJ, Lips KR & Bermingham E (2010) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences* 107: 13777-13782.
- Crichton M (1991) *Jurassic Park*. Random House Publishing Group, New York, USA. 1-464.
- Crowe TM & Crowe AA (1982) Patterns of distribution, diversity and endemism in Afrotropical birds. *Journal of Zoology* 198: 417-442.
- Daszak P, Berger L, Cunningham AA, Hyatt AD, Green DE & Speare R (1999) Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5: 735-748.
- Daszak P, Cunningham AA & Hyatt AD (2003) Infectious disease and amphibian population declines. *Diversity and Distributions* 9: 141-150.
- Daversa D, Bosch J & Jeffery K (2011) First survey of the chytrid fungus, *Batrachochytrium dendrobatidis*, in amphibian populations from Gabon, Africa. *Herpetological Review* 42: 67-69.
- De Klerk HM, Crowe TM, Fjeldså & Burgess ND (2002a) Biogeographical patterns of endemic terrestrial Afrotropical birds. *Diversity and Distributions* 8: 147-162.
- De Klerk HM, Crowe TM, Fjeldså & Burgess ND (2002b) Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical region. *Journal of Zoology* 256: 327-342.
- De la Riva I (1994) Anfibios anuros del Parque Nacional de Monte Alén, Río Muni, Guinea Ecuatorial. *Revista Espanola de Herpetologia* 8: 123-139.
- De Marco P, Diniz-Filho JAF & Bini LM (2008) Spatial analysis improves species distribution modelling during range expansion. *Biology Letters* 4: 577-580.
- De Menocal PB (1995) Plio-Pleistocene African climate. *Science*, 270, 53-59.
- Diamond AW & Hamilton AC (1980) The distribution of forest passerine birds and quaternary climatic change in Africa. *Journal of Zoology* 191: 379-402.
- Doherty-Bone TM, Gonwouo NL, Hirschfeld M, Ohst T, Weldon C, Perkins M, Kouete MT, Browne RK, Loader SP, Gower, Wilkinson MW, Rödel M-O, Penner J, Barej MF, Schmitz A, Plötner J & Cunningham AA (2013) *Batrachochytrium dendrobatidis* in amphibians of Cameroon, including first records of infected caecilian hosts. *Diseases of Aquatic Organisms* 102: 187-194.
- Dole JW (1971) Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* 1971: 221-228.
- Drew A, Allen EJ & Allen LJS (2006) Analysis of climatic and geographic factors affecting the presence of chytridiomycosis in Australia *Diseases of Aquatic Organisms* 68: 245-250.
- Drewes RC & Vindum JV (1994) Amphibians of the Impenetrable Forest, Southwest Uganda. *Journal of African Zoology* 108: 55-70.
- Drewes RC (1984) Aphylogenetic analysis of the Hyperoliidae (Anura): Treefrogs of Africa, Madagascar, and the Seychelles Islands. *Occasional Papers of the California Academy of Sciences* 139: 1-70.
- Dubois A (1995) Keratodont formula in anuran tadpoles: proposals for a standardization. *Journal of Zoological Systematic and Evolutionary Research* 33: I-XV.
- Duellman WE & Trueb L (1994) *Biology of the amphibians*. The John Hopkins University Press, Baltimore, USA. 1-670.
- Dupanloup I, Schneider S & Excoffier L (2002) A simulated annealing approach to define the genetic structure of populations. *Molecular Ecology* 11: 2571-2581.



- Dupont LM, Jahns S, Marret F & Ning S (2000) Vegetation change in equatorial Africa: time-slices for the last 150 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology* 155: 95-122.
- El Mouden EH, Slimani T, Donaire D, Fernández-Beaskoetxea S, Fisher MC & Bosch J (2011) First record of the chytrid fungus *Batrachochytrium dendrobatidis* in North Africa. *Herpetological Review* 42: 71-75.
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann G, Loiselle BA, Manion G, Moritz G, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS & Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE & Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43-57.
- Emms C, Jambang MDK, Bah O, Mankali B, Rödel M-O & Barnett L (2006) The amphibian fauna of The Gambia, West Africa. *Herpetological Bulletin* 94: 6-16.
- Endler JA (1982) Pleistocene forest refuges: fact or fancy? In: Prance GT (ed) *Biological diversification in the tropics*. Columbia University Press, New York, USA. 641-657.
- Eniang EA & Luiselli L (2002) Ikpan wetland rainforest: an area of high biodiversity importance in south-eastern Nigeria. *Revue Écologie (Terre Vie)* 57: 19-28.
- Ernst R & Rödel M-O (2005) Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86: 3111-3118.
- Ernst R & Rödel M-O (2006) Community assembly and structure of tropical leaf-litter anurans. *Ecotropica* 12: 113-129.
- Ernst R & Rödel M-O (2008) Patterns of community composition in two tropical tree frog assemblages: separating spatial structure and environmental effects in disturbed and undisturbed forests. *Journal of Tropical Ecology* 24: 111-120.
- Ernst R, Agyei AC & Rödel M-O (2005) Herpetological assessment of Draw River, Boi-Tano, and Krokosua Hills. In: McCullough J, Decher J & Guba-Kpelle D (eds) *A biological assessment of the terrestrial ecosystems of the Draw River, Boi-Tano, Tano Nimiri and Krokosua Hills forest reserves, southwestern Ghana*. RAP Bulletin of Biological Assessment 36, Conservation International, Washington DC, USA. 44-49, app. 5-7: 137-141.
- Ernst R, Linsenmair KE & Rödel M-O (2006) Diversity erosion beyond the species level: Dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biological Conservation* 133: 143-155.
- Euzet L, Combaz C & Knoepffler L-P (1969) Parasites d'amphibiens de Côte d'Ivoire et du Liberia: Polystomatidae (Monogenea). *Biologia Gabonica* 3: 217-221.
- Falk TM, Teugels GG, Abban EK, Villwock W & Renwartz L (2003) Phylogeographic patterns in populations of the black-chinned Tilapia complex (Teleostei, Cichlidae) from coastal areas in West Africa: support for the refuge zone theory. *Molecular Phylogenetics and Evolution* 27: 81-92.
- Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimanda J, Umland J, Werner M, Oskin M, Alsdorf Det al. (2007) The shuttle radar topography mission. *Reviews of Geophysics* 45: 1-33.
- Farrer RA, Weinert LA, Bielby J, Garner TWJ, Balloux F, Clare F, Bosch J, Cunningham AA, Weldon C, du Preez LH, Anderson L, Pond SLK, Shahar-Golan R, Henk DA & Fisher MC (2011) Multiple emergences of genetically diverse amphibian infecting chytrids include a globalized hypervirulent recombinant lineage. *Proceedings of the National Academy of Sciences* 108: 18732-18736.
- Finch J, Leng MJ & Marchant R (2009) Late quaternary vegetation dynamics in a biodiversity hotspot, the Uluguru Mountains of Tanzania. *Quaternary Research* 72: 111-122.
- Fisher MC & Garner TWJ (2007) The relationship between the emergence of *Batrachochytrium dendrobatidis*, the international trade in amphibians and introduced amphibian species. *Fungal Biology Review* 21: 2-9.
- Fisher MC, Garner TWJ & Walker SF (2009) Global emergence of *Batrachochytrium dendrobatidis* and amphibian Chytridiomycosis in space, time, and host. *Annual Review of Microbiology* 63: 291-310.
- Fjeldsø J (1994) Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* 3: 207-226.
- Ford J (1971) *The role of the Trypanosomiases in African ecology: A study of the tsetse fly problem*. Clarendon Press, Oxford, UK. 1-568.
- Franklin J (2009) *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press, Cambridge, UK. 1-338.
- Frétey T & Blanc CP (2000) Liste des Amphibiens d'Afrique centrale. Cameroun, Congo, Gabon, Guinée-Equatoriale, République Centrafricaine, République Démocratique du Congo, São Tomé et Príncipe. Les dossiers de l'ADIE, Série Biodiversité N°2: 1-39.



- Frétey T & Dewynter M (1998) Amphibiens anoures de la Forêt des Abeilles (Gabon). *Journal of African Zoology* 112: 171-184.
- Frost DR (2007) Amphibian species of the World: an online reference. Version 5.0 (1 February 2007). <http://research.amnh.org/herpetology/amphibia/index.php> (last accessed 20 August 2008).
- Frost DR (2010) Amphibian species of the World: an online reference. Version 5.4 (8 April 2010). <http://research.amnh.org/herpetology/amphibia/index.php> (last accessed 25 July 2010).
- Frost DR (2011) Amphibian Species of the World: an online Reference. Version 5.5. <http://research.amnh.org/vz/herpetology/amphibia/> (last accessed 28 February 2012).
- Frost DR (2013) Amphibian Species of the World: an online Reference. Version 5.6 (9 January 2013).). Available from <http://research.amnh.org/herpetology/amphibia/index.php> (last accessed 6 December 2013).
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM & Wheeler WC (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1-370.
- Funk WC, Greene AE, Corn PS & Allendorf FW (2005) High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biology Letters* 1: 13-16.
- Furse MT, Moss D, Wright JF & Armitage PD (1984) The influence of seasonal and taxonomic factors on the ordination and classification of running-water sites in Great Britain and on the prediction of their macro-invertebrate communities. *Freshwater Biology* 14: 257-280.
- Garland S, Wood J, Skerratt L (2011) Comparison of sensitivity between realtime detection of a TaqMan assay for *Batrachochytrium dendrobatidis* and conventional detection. *Diseases of Aquatic Organisms* 94: 101-105.
- Garmyn A, Van Rooij P, Pasmans F, Hellebuyck T, Van Den Boeck W, Haesebrouck F & Martel A (2012) Waterfowl: Potential environmental reservoirs of the chytrid fungus *Batrachochytrium dendrobatidis*. *PLoS One* 7: e35038.
- Garner TWJ, Perkins MW, Govindarajulu P, Seglie D, Walker SF, Cunningham AA & Fisher F (2006) The emerging amphibian pathogen *Batrachochytrium dendrobatidis* globally infects introduced populations of the North American bullfrog, *Rana catesbeiana*. *Biology Letters* 2: 455-459.
- Gascon C, Loughheed SC & Bogart JP (1998) Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. *Biotropica* 30: 104-119.
- Gaston K.J. (2003) The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK. 1-282.
- GBIF (2013) last accessed 27 May 2013 through GBIF data portal; <http://data.gbif.org/datasets/resource/>... (resource numbers are listed after the respective institution; CAS Herpetology (HERP) 14129; Ditsong Museum 11955; SMNS Herpetologie 14192; Museum of Comparative Zoology, Harvard University 14100; RBINS collections 13690; Paleobiology Database 563; Partial Amphibians Collection 14159; MVZ Herp Collection 14800; Albany Museum 11950; NMNH Vertebrate Zoology Herpetology Collections 1838; Peabody Herpetology DiGIR Service 1825; iNaturalist research-grade observations 14026; Terrestrial vertebrates 1465; Colección Nacional de Herpetología - Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' 9114; LACM Vertebrate Collection 14305; Macaulay Library - Audio Data 41; South Australian Museum Australia provider for OZCAM 14121; Herp specimens, 659; Herpetology Collection - Royal Ontario Museum 14792; Amphibians and Reptiles collection at the Natural History Museum of Denmark (SNM) 14021; Collection Herpetology SMF 8309; RMCA-HERP 1740; Tanzanian Vertebrate Collection 1891; Herpetology Collection 14838; KUBI Herpetology Collection 14487; UTEP Vertebrates 14396; Amphibians and Reptiles 1900; Amphibian specimens 12787; University of Alberta Museums Amphibian and Reptile Collection 2466; CUMNH Herpetology Collection 2556; CUMV Amphibian Collection 14896; SysTax - Zoological Collections 14439; NRM-Herpetology 1036; Herpetile collection Natural History Museum University of Oslo 8103; Herps 9103; Rapid Assessment Program (RAP) Biodiversity Survey Database 8076; UWBM Herpetology Collection (Arctos) 14864; Animal Sound Archive 14719; Museu de Ciències Naturals de Barcelona: MCNB-Cord 9126; Estación Experimental de Zonas Áridas (CSIC): EEZA-Herpet 11263)
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE & Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378-383.
- Gibson LA (2011) The importance of incorporating imperfect detection in biodiversity assessments: a case study of small mammals in an Australian region. *Diversity and Distributions* 17: 613-623.
- Global Witness Report (2012) Signing their lives away: Liberia's private use permits and the destruction of community-owned rainforest. Report September 2012: 1-11.
- Goater CP, Semlitsch RD & Bernasconi MV (1993) Effects of body size and parasite infection on the locomotory performance of juvenile toads, *Bufo bufo*. *Oikos* 66: 129-136.
- Goka K, Yokoyama J, Une Y, Kuroki T, Suzuki K, Nakahara M, Kobayashi A, Inaba S, Mizutani T & Hyatt AD (2009) Amphibian chytridiomycosis in Japan: distribution, haplotypes and possible route of entry into Japan. *Molecular Ecology* 18: 4757-4774.
- Goldberg TL, Read AM & Lee MH (2007) Chytrid Fungus in Frogs from an Equatorial African Montane Forest in western Uganda. *Journal of Wildlife Diseases* 43: 521-524.



- Gordon AD & Vichi M (2001) Fuzzy partition models for fitting a set of partitions. *Psychometrika* 66: 229-248.
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183-190.
- Goudie AS (2005) The drainage of Africa since the Cretaceous. *Geomorphology* 67: 437-456.
- Gower DJ, Doherty-Bone TM, Aberra RK, Mengistu A, Schwaller S, Menegon M, de Sá R, Saber SA, Cunningham AA & Loader SP (2012) High prevalence of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) across multiple taxa and localities in the highlands of Ethiopia. *Herpetological Journal* 22: 225-233.
- Grafe TU & Linsenmair KE (1989) Protogynous sex change in the reed frog *Hyperolius viridiflavus*. *Copeia* 1989: 1024-1029.
- Grafe TU, Döbler S & Linsenmair KE (2002) Frogs flee from the sound of fire. *Proceedings of the Royal Society of London B* 269: 999-1003.
- Grafe TU, Stewart MM, Lampert KP, Rödel M-O (2011) Putting toe clipping into perspective: A viable method for marking anurans. *Journal of Herpetology* 45: 28-35.
- Greenbaum E & Carr JL (2005) The herpetofauna of Upper Niger National Park, Guinea, West Africa. *Scientific Papers of the Natural History Museum University of Kansas* 37: 1-21.
- Greenbaum E, Kusamba C, Aristote MM & Reed K (2008) Amphibian chytrid fungus infections in *Hyperolius* (Anura: Hyperoliidae) from eastern Democratic Republic of Congo. *Herpetological Review* 39: 70-73.
- Grenyer R Orme CDL, Jackson SF, Thomas GH, Davies RG, Davies TJ, Jones KE, Olson VA, Ridgely RS, Rasmussen PC, Ding T-S, Bennett PM, Blackburn TM, Gaston KJ, Gittleman JL & Owens IPF (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature* 444: 93-96.
- Griffith DA (2003) Spatial autocorrelation and spatial filtering: gaining understanding through theory and scientific visualization. Springer Verlag, Berlin, Germany. 1-250.
- Grubb P (1992) Refuges and dispersal in the speciation of African forest mammals. In: Prance GT (ed) *Biological diversification in the tropics*. Columbia University Press, New York, USA. 537-543.
- Gschweng M, Kalko EKV, Berthold P, Fiedler W & Fahr J (2012) Multi-temporal distribution modelling with satellite tracking data: predicting responses of a long-distance migrant to changing environmental conditions. *Journal of Applied Ecology* 49: 803-813.
- Guibé J & Lamotte M (1958) La réserve naturelle intégrale du Mont Nimba. XII. Batraciens (sauf *Arthroleptis*, *Phrynobatrachus* et *Hyperolius*). *Mémoires de l'Institut fondamental d'Afrique noire* 53: 241-273.
- Guibé J & Lamotte M (1963) La réserve naturelle intégrale du Mont Nimba. XXVIII. Batraciens du genre *Phrynobatrachus*. *Mémoires de l'Institut fondamental d'Afrique noire* 66: 601-627.
- Guibé J (1950) Catalogue des types d'amphibiens du Muséum national d'Histoire naturelle. Nationally printed, Paris, France. 1-71.
- Guindon S & Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696-704.
- Hacker JE, Cowlishaw G & Williams PH (1998) Patterns of African primate diversity and their evaluation for the selection of conservation areas. *Biological Conservation* 84: 251-262.
- Haffer J (1969) Speciation in Amazonian forest birds. *Science* 165: 131-137.
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- Hamilton AC & Taylor D (1991) History of climate and forests in tropical Africa during the last 8 million years. *Climatic Change* 19: 65-78.
- Hamilton AC (1976) The Significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of Upper Pleistocene palaeoenvironments: a review. *Palaeoecology of Africa* 9: 63-97.
- Hansen LA, Burgess ND, Fjeldså J & Rahbek C (2009) The Copenhagen databases of African vertebrates. <http://130.225.211.158/SubsaharanAfrica/mappinginfo.html> (last accessed 2 September 2010).
- Hansen M, DeFries R, Townshend JR, Carroll M, Dimiceli C & Sohlberg R (2003a) Vegetation Continuous Fields MOD44B, 2001 Percent bare ground cover, Collection 3, Maryland, University of Maryland, College Park.
- Hansen M, DeFries R, Townshend JR, Carroll M, Dimiceli C & Sohlberg R (2003b) Vegetation Continuous Fields MOD44B, 2001 Percent herbaceous ground cover, Collection 3, Maryland, University of Maryland, College Park.
- Hansen M, DeFries R, Townshend JR, Carroll M, Dimiceli C & Sohlberg R (2003c) Vegetation Continuous Fields MOD44B, 2001 Percent tree cover, Collection 3, Maryland, University of Maryland, College Park.



- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehmann SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO & Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342: 850-853.
- Hansen MC, Stehman SV, Potapov PV, Loveland TR, Townshend JRG, DeFries RS, Pittman KW, Arunarwati B, Stolle F, Steininger MK, Carroll M & DiMiceli C (2008) Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences* 105: 9439-9444.
- Harcourt CS, Davies D, Waugh J, Oates J, Coulthard N, Burgess N, Wood P & Palmer P (1992) Sierra Leone. In: Sayer JA, Harcourt CS & Collins NM (eds) *The conservation atlas of tropical forests: Africa*. Macmillan Publishers Ltd, Basingstoke, UK. 244-250.
- Heard M, Smith KF & Ripp K (2011) Examining the evidence for chytridiomycosis in threatened amphibian species. *PLoS One* 6: e23150.
- Heikkinen RK, Marmion M & Luoto M (2011) Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* 35: 276-288.
- HerpNet (2013) last accessed 22 May 2013 through <http://www.herpnet.org/portal.html> (data provided by the following institutions, abbreviations after HerpNet: BLB; CAS; CM; CUMV, KU; LACM; MCZ; MPM; MVZ; PSM; RMCA; RMMU; ROM; SDNHM; SMNS, UA; UBCBBM; UCM; USNM; UWBM; YPM; ZIN).
- Herrmann H-W, Böhme W, Herrmann PA, Plath M, Schmitz A & Solbach M (2005) African biodiversity hotspots: the amphibians of Mt. Nlonako, Cameroon. *Salamandra* 41: 61-81.
- Herrmann H-W, Schmitz A, Herrmann PA & Böhme W (2006) Amphibians and reptiles of the Tchabal Mbabo Mountains, Adamaoua Plateau, Cameroon. *Bonner zoologische Beiträge* 55: 27-35.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG & Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.
- Hillers A & Rödel M-O (2007) Rapid survey of amphibians and reptiles of North Lorma, Gola and Grebo National Forests. In: Hoke P, Demey R & Peal A (eds) *A rapid biological assessment of North Lorma, Gola and Grebo National Forests, Liberia*. RAP Bulletin of Biological Assessment 44, Washington DC, USA. 29-33 & 86-92.
- Hillers A & Rödel M-O (2007) The amphibians of three national forests in Liberia, West Africa. *Salamandra*, 43: 1-10.
- Hillers A (2008) West African forest frogs - ecology, evolution, and conservation. Unpublished PhD thesis, University of Amsterdam, The Netherlands. 1-182.
- Hillers A, Bangoura MA, Loua N-S & Rödel M-O (2006) Inventaire rapide des amphibiens et des reptiles dans la région de Boké dans le nord-ouest de la Guinée. In: Wright HE, McCullough J, Diallo MS (eds) *Une inventaire biologique rapide de la préfecture de Boké dans le nord-ouest de la Guinée / A rapid biological assessment of Boké Préfecture, northwestern Guinea*. RAP Bulletin of Biological Assessment 41, Conservation International, Washington DC. 59-64, 131-136, 178-181.
- Hillers A, Boateng CO, Segniagbeto GH, Agyei AC & Rödel M-O (2009) Assessment of the amphibians in the forests of southern Ghana and western Togo. *Zoosystematics and Evolution* 85: 127-141.
- Hillers A, Loua N-S & Rödel M-O (2008b) A preliminary assessment of the amphibians of the Fouta Djallon, Guinea, West Africa. *Salamandra* 44: 113-122.
- Hillers A, Loua N-S & Rödel M-O (2008d) Assessment of the distribution and conservation status of the viviparous toad *Nimbaphrynoides occidentalis* on Monts Nimba, Guinea. *Endangered Species Research* 5: 13-19.
- Hillers A, Veith M & Rödel M-O (2008c) Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conservation Biology* 22: 762-772.
- Hillers A, Zimkus B & Rödel M-O (2008a) A new *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from north-western Guinea, West Africa. *Zootaxa* 1815: 43-50.
- Hoogmoed MS (1980) Herpetologische waarnemingen in Ghana II. *Lacerta* 38: 10-20.
- Hopkins S & Channing A (2003) Chytrid fungus in northern and western Cape frog populations, South Africa. *Herpetological Review* 34: 334-336.
- Hornik K (2009) Package 'clue', version 03-27.
- Howell KM (1993) Herpetofauna of the Eastern African forests. In: Lovett JC & Wasser SK (eds) *Biogeography and ecology of the rain forests of Eastern Africa*. Cambridge University Press, Cambridge, UK. 173-203.
- Huelsenbeck JP & Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754-755.
- Hughes B (1988) Herpetology in Ghana (West Africa). *British Herpetological Society Bulletin* 25: 29-38.
- Hugueny B & Lévêque C (1994) Freshwater fish zoogeography in West Africa - faunal similarities between river basins. *Environmental Biology of Fishes* 39: 365-380.



- Hugueny B & Lévêque C (1994) Freshwater zoogeography on west Africa: faunal similarities between river basins. *Environmental Biology of Fishes* 39: 365-380.
- Hulselmans JLJ (1971) Contribution à l'herpétologie de la République du Togo, 4. Description de *Conraua derooi*, n. sp. (Amphibia). *Revue Zoologique Botanique Africaine* 84: 153-159.
- Hurlbert AH & Jetz W (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences* 104: 13384-13389.
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415-427.
- Hyatt AD, Boyle DG, Olsen V, Boyle DB, Berger L, Obendorf D, Dalton A, Kriger K, Hero M, Hins H, Phillott R, Campbell R, Marantelli G, Gleason F & Coiling A (2007) Diagnostic assays and sampling protocols for the detection of *Batrachochytrium dendrobatidis*. *Diseases of Aquatic Organisms* 73: 175-192.
- Imasuen AA, Aisen MSO, Weldon C, Dalton DL, Kotze A & du Preez LH (2011) Occurrence of *Batrachochytrium dendrobatidis* in Amphibian Populations of Okomu National Park, Nigeria. *Herpetological Review* 42: 379-382.
- Imasuen AA, Weldon C, Aisien MSO & du Preez LH (2009) Amphibian chytridiomycosis: first report in Nigeria from the skin slough of *Chiromantis rufescens*. *Froglog* 90: 6-8.
- Intierra Mapping (2008) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- Intierra Mapping (2009) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- Intierra Mapping (2010) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- Intierra Mapping (2011) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- Intierra Mapping (2012) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- Intierra Mapping (2013) West Africa - Mining and exploration activity. IntierraRMG. 1map.
- IPCC (2013) Intergovernmental panel on climate change. <http://www.ipcc.ch> (last accessed 6 December 2013),
- Isaac NJB, Redding DW, Meredith HM & Safi K (2012) Phylogenetically-informed priorities for amphibian conservation. *PLoS ONE* 7: e43912.
- Isaac NJB, Turvey ST, Collen B, Waterman C & Baillie JEM (2007) Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. *PLoS ONE* 2: e296.
- IUCN (2008) IUCN Red List of threatened species - Update. <http://www.iucnredlist.org> (last accessed on 6 December 2013)
- IUCN (2010) IUCN Red List of threatened species. Version 2010.3. <http://www.iucnredlist.org> (last accessed on 2 September 2010).
- IUCN (2011) IUCN Red List of threatened species. Version 2011.2. <http://www.iucnredlist.org> (last accessed 28 February 2012).
- IUCN (2013) IUCN Red List of threatened species. Version 2013.1. <http://www.iucnredlist.org> (last accessed 31 July 2013).
- IUCN, Conservation International & NatureServe (2004) Global Amphibian Assessment. <http://www.globalamphibians.org> (last accessed 19 August 2008).
- Jaccard P (1908) Nouvelles recherches sur la distribution florale. *Bulletin de la Societe Vaudoise Sciences Naturelles* 44: 223-270.
- Jackson K & Blackburn DC (2007) The amphibians and reptiles of Nouabale-Ndoki National Park, Republic of Congo (Brazzaville). *Salamandra* 43: 149-164.
- Jackson K, Zassi-Boulou A-G, Mavoungou LB & Pangou S (2007) Amphibians and reptiles of the Lac Télé community reserve, Likouala region, Republic of Congo (Brazzaville). *Herpetological Conservation and Biology* 2: 75-86.
- Jameson DL (1956) Growth, dispersal and survival of the Pacific tree frog. *Copeia* 1956: 25-29.
- Jetz W & Rahbek C (2001) Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences* 98: 5661-5666.
- Jetz W & Rahbek C (2002) Geographic range size and determinants of avian species richness. *Science* 297: 1548-1551.
- Jetz W, Sekercioglu CH & Watson JEM (2007) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology* 22: 110-119.
- Joger U & Lambert MRK (2002) Inventory of amphibians and reptiles in SE Senegal, including the Niokola-Koba National Park, with observations on factors influencing diversity. *Tropical Zoology* 15: 165-185.



- Joger U (1990) The herpetofauna of the Central African Republic, with description of a new species of *Rhinotyphlops* (Serpentes: Typhlopidae). In: Peters G & Hutterer R (eds) Vertebrates in the tropics. Museum Alexander Koenig, Bonn, Germany. 85-102.
- John DM (1986) The inland waters of tropical West Africa: an introduction and botanical review. *Advances in Limnology* 23: 1-244.
- Johnson ML & Speare R (2005) Possible modes of dissemination of the amphibian chytrid *Batrachochytrium dendrobatidis* in the environment. *Diseases of Aquatic Organisms* 65: 181-186.
- Johnson ML, Berger L, Philips L & Speare R (2003) Fungicidal effects of chemical disinfectants, UV light, desiccation and heat on the amphibian chytrid *Batrachochytrium dendrobatidis*. *Diseases of Aquatic Organisms* 57: 255-260.
- Jombart T (2008) ADEGENET: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24: 1403-1405.
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427-2439.
- Jost L (2010) Independence of alpha and beta diversities. *Ecology* 91: 1969-1974.
- Kareiva P & Marvier M (2003) Conserving biodiversity coldspots. *American Scientist* 91: 344-351.
- Kéry M (2002) Inferring the absence of a species - a case studies of snakes. *Journal of Wildlife Management* 66: 330-338.
- Kielgast J, Rödder D, Veith M & Lötters S (2010) Widespread occurrence of the amphibian chytrid fungus in Kenya. *Animal Conservation* 13: 1-8.
- Kilburn VL, Ibáñez R & Green DM (2011) Reptiles as potential vectors and hosts of the amphibian pathogen *Batrachochytrium dendrobatidis* in Panama. *Diseases of Aquatic Organisms* 97: 127-134.
- Kilpatrick AM, Briggs CJ & Daszak P (2009) The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology and Evolution* 25: 109-118.
- Kingdon J (1990) *Island Africa: evolution of Africa's animals and plants*. Collins, London, UK. 1-287.
- Kinney VC, Heemeyer JL, Pessier AP & Lannoo MJ (2011) Seasonal Pattern of *Batrachochytrium dendrobatidis* infection and mortality in *Lithobates areolatus*: Affirmation of Vredenburg's "10,000 Zoospore Rule". *PLoS One* 6: e16708.
- Kouamé NG, Boateng CO & Rödel M-O (2007) A rapid survey of the amphibians from the Atewa Range Forest Reserve, Eastern Region, Ghana. In: McCullough J, Alonso LE, Naskrecki P, Wright HE & Osei-Owusu Y (eds) *A rapid biological assessment of the Atewa Range Forest Reserve, Eastern Ghana*. RAP Bulletin of Biological Assessment 47, Conservation International, Washington DC, USA. 76-83.
- Kouame OML, Jengre N, Kobele M, Knox D, Ahon DB, Gbondo J, Gamys J, Egnankou W, Siaffa D, Okoni-Williams A & Saliou M (2012) Key biodiversity areas identification in the Upper Guinea forest biodiversity hotspot. *Journal of Threatened Taxa* 4: 2745-2752.
- Kreft H & Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography* 37: 2029-2053.
- Krell F-T (2004) Parataxonomy vs. taxonomy in biodiversity studies - pitfalls and applicability of "morphospecies" sorting. *Biodiversity and Conservation* 13: 795-812.
- Kruger KM & Hero J-M (2007a) Large-scale seasonal variation in the prevalence and severity of chytridiomycosis. *Journal of Zoology* 271: 352-359.
- Kruger KM & Hero J-M (2007b) The chytrid fungus *Batrachochytrium dendrobatidis* is non-randomly distributed across amphibian breeding habitats. *Diversity and Distributions* 13: 781-788.
- Kruger KM & Hero J-M (2009) Chytridiomycosis, amphibian extinctions, and lessons for the prevention of future panzootics. *EcoHealth* 6: 6-10.
- Kruskal JB & Wish M (1978) *Multidimensional scaling*. Sage Publications, Beverley Hills, USA. 1-96.
- Kukkula AS & Moilanen A (2013) Core concepts of spatial prioritisation in systematic conservation planning. *Biological Reviews* 88: 443-464.
- Küper W, Sommer JH, Lovett JC, Mutke J, Linder HP, Beentje HJ, van Rompaey RASR, Chatelain C, Sosef M & Barthlott W (2004) Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden* 91: 525-536.
- Lamirande EW & Nichols DK (2002) Effects of host age on susceptibility to cutaneous chytridiomycosis in blue- and yellow poison dart frogs (*Dendrobates tinctorius*). In: McKinnell RG & Carlson DL (eds) *Proceeding of the sixth international symposium on the pathology of reptiles and amphibians*. University of Minnesota, Minnesota, USA. 3-16.
- Lamotte M & Xavier F (1966) Étude comparée de deux espèces de *Phrynobatrachus* souvent confondues: *Phr. plicatus* Günther et *Phr. auritus* Boulenger. *Bulletin de l'Institut fondamental d'Afrique noire, Sér. A* 28: 1605-1619.



- Lamotte M & Zuber-Vogeli M (1954) Contribution à l'étude des batraciens de l'Ouest Africain III.– Le développement larvaires de deux espèces rhéophiles, *Astylosternus diadematus* et *Petropedetes natator*. Bulletin de l'Institut fondamental d'Afrique noire, Sér. A 16: 1222-1233.
- Lamotte M (1966) Types de répartition géographique de quelques batraciens dans l'Ouest Africain. Bulletin de l'Institut fondamental d'Afrique noire Sér. A 28: 1140-1148.
- Lamotte M (1967) Les batraciens de la région de Gpakobo (Côte d'Ivoire). Bulletin de l'Institut fondamental d'Afrique noire Sér. A 29: 218-294.
- Lamotte M (1969) Le parc national du Niokolo–Koba, Fasciule III; XXX. Amphibiens (deuxième note). Mémoires de l'Institut fondamental d'Afrique noire 84: 420-426.
- Lamotte M (1971) Le Massif des Monts Loma (Sierra Leone), Fasciule I; XIX. Amphibiens. Mémoires de l'Institut fondamental d'Afrique noire 86: 397-407.
- Lampert KP & Linsenmair KE (2002) Alternative life cycle strategies in the West African reed frog *Hyperolius nitidulus*: the answer to an unpredictable environment? *Oecologia* 130: 364-372.
- Lampert KP, Rand AS, Mueller UG & Ryan MJ (2003) Fine-scale genetic pattern and evidence for sex-biased dispersal in the túngara frog, *Physalaemus pustulosus*. *Molecular Ecology* 12: 3325-3334.
- Lane E, Weldon C & Bingham J (2003) Histological evidence of chytridiomycosis in a free-ranging amphibian (*Afrana fuscigula* (Anura: Ranidae)) in South Africa. *Journal of the South African Veterinary Association* 74: 20-21.
- Largen MJ & Dowsett-Lemaire F (1991) Amphibians (Anura) from the Kouilou River Basin, République du Congo. Tauraco Research Report: 4 145-168.
- Larsen FW & Rahbek C (2003) Influence of scale on conservation priority setting - a test on African mammals. *Biodiversity and Conservation* 12: 599-614.
- Larsen FW, Turner WR & Brooks TM (2012) Conserving critical sites for biodiversity provides disproportionate benefits to people. *PLoS ONE* 7: e36971.
- Laube I, Korntheuer H, Schwager M, Trautmann S, Rahbek C & Böhning-Gaese K (2013) Towards a more mechanistic understanding of traits and range sizes. *Global Ecology and Biogeography* 22: 233-241.
- Laurent RF (1951a) Catalogue des rainettes africaines (genres *Afraxalus* et *Hyperolius*) de la collection du Muséum National d'Histoire Naturelle de Paris. *Annales de la Société Royale Zoologique de Belgique* 82: 23-50.
- Laurent RF (1951b) Quelques données nouvelles sur la systématique et l'écologie du genre *Hyperolius* Rapp. *Annales de la Société Royale Zoologique de Belgique* 82: 329-337.
- Laurent RF (1951c) Aperçu des formes actuellement reconnaissables dans la superespèce *Hyperolius marmoratus*. *Annales de la Société Royale Zoologique de Belgique* 82: 379-397.
- Laurent RF (1961) Note sur les *Hyperolius* et quelques *Afraxalus* (Salientia) du Musée de Berlin. *Revue de zoologie et de botanique africaines* 64: 65-96.
- Laurent RF (1973) A parallel survey of equatorial amphibians and reptiles in Africa and South America. In: Meggers BJ, Ayensu ES & Duckworth WD (eds) *Tropical forest ecosystems in Africa and South America - a comparative review*. Smithsonian Institution Press, Washington, DC, USA. 259-266.
- Laurent RF (1976) Nouveaux commentaires sur la superespèce *Hyperolius viridiflavus* (Anura). *Musée Royal d'Afrique Centrale Série IN-8, Science zoologique* 213: 71-114.
- Laurent RF (1983) La superespèce *Hyperolius viridiflavus* (Duméril & Bibron, 1841) (Anura Hyperoliidae) en Afrique Centrale. *Monitore Zoologico Italiano N.S. Suppl.* 18: 1-93.
- Lawson DP (1993) The reptiles and amphibians of the Korup National Park project, Cameroon. *Herpetological Natural History* 1: 27-90.
- Lea JM, Luiselli L & Politano E (2005) Are there shifts in amphibian faunal composition in Nigerian landscapes undergoing long-term degradation? A case study from a montane environment. *Revue Écologie (Terre Vie)* 60: 65-76.
- Lea MJ, Politano E & Luiselli L (2003) Changes in the herpetofauna of a fresh water river in southern Nigeria, after 20 years of development. *Russian Journal of Herpetology* 10: 191-198.
- Leaché AD & Boateng CO (2009) A Rapid Survey of the Amphibians and Reptiles of Ajenjua Bepo and Mamang River Forest Reserves, Eastern Region of Ghana. In: McCullough J, Hoke P, Naskrecki P & Osei-Owusu Y (eds) *A rapid biological assessment of the Ajenjua Bepo and Mamang River Forest Reserves, Ghana. RAP Bulletin of Biological Assessment* 50, Conservation International, Washington DC, USA. 46-49.
- Leaché AD (2005) Results of a herpetological survey in Ghana and a new country record. *Herpetological Review* 36: 16-19.
- Leaché AD, Rödel M-O, Linkem CW, Diaz RE, Hillers A, Fujita MK (2006) Biodiversity in a forest island: reptiles and amphibians of the West African Togo Hills. *Amphibian and Reptile Conservation* 4: 22-45.



- Learner MA, Densem JW & Iles TC (1983) A comparison of some classification methods used to determine benthic macro-invertebrate species associations in river survey work based on data obtained from the River Ely, South Wales. *Freshwater Biology* 13: 13-36.
- Legendre P & Legendre L (1998) *Numerical ecology*, 2nd ed. Elsevier Science B.V., Amsterdam, The Netherlands. 1-853.
- Leibold MA (1995) The niche concept revisited: mechanistic models and community context. *Ecology* 76: 1371-1382.
- Lester SE, Ruttenberg BI, Gaines SD & Kinlan BP (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters* 10: 745-758.
- Leyer I & Wesche K (2007) *Multivariate Statistik in der Ökologie - Eine Einführung*. Springer Verlag, Berlin, Germany. 1-232.
- Li R, Chen W & Fu J (2009) Rivers as barriers for high elevation amphibians: a phylogeographic analysis of the alpine stream frog of the Hengduan Mountains. *Journal of Zoology* 277: 309-316.
- Linder HP (2001) Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* 28: 169-182.
- Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldsø J & Rahbek C (2012) The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography* 39: 1189-1205.
- Linsenmair KE (1998) Risk-spreading and risk-reducing tactics of West African anurans in an unpredictably changing and stressful environment. In: Newbery DM, Prins HHT & Brown ND (eds) *Dynamics of tropical communities*. Blackwell Science, London, UK. 221-242.
- Lips KR (1999) Mass mortality and population declines of Anurans at an upland site in western Panama. *Conservation Biology* 13: 117-125.
- Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, Carey C, Livo L, Pessier AP & Collins JP (2006) Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences* 103: 3165-3170.
- Lips KR, Diffendorfer J, Mendelson III JR & Sears MW (2008) Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS Biol* 6: e72.
- Lips KR, Mendelson III JR, Muñoz-Alonso A, Canseco-Márquez L & Mulcahy DG (2004) Amphibian population declines in montane southern Mexico: resurveys of historical localities. *Biological Conservation* 119: 555-564.
- Loader SP, Poynton JC, & Mariaux J (2004) Herpetofauna of Mahenge Mountains, Tanzania: a window on African biogeography. *African Zoology* 39: 1-6.
- Lomolino MV, Sax DF & Brown JH (2004) *Foundations of biogeography*. The University of Chicago Press, Chicago, USA. 1-1328.
- Longcore JR, Longcore JE, Pessier AP & Halteman WA (2007) Chytridiomycosis widespread in anurans of north eastern United States. *Journal of Wildlife Management* 71: 435-444.
- Lötters S, Kielgast J, Bielby J, Schmidtlein S, Bosch J, Veith M, Walker SF, Fisher MC & Rödder D (2010) The link between rapid enigmatic amphibian decline and the globally emerging chytrid fungus. *EcoHealth* 6: 358-372.
- Lötters S, Wagner P, Bwong BA, Schick S, Malonza PK, Muchai V, Wasonga DV & Veith M (2007) *A fieldguide to the amphibians and reptiles of the Kakamega Forest. Kielezo cha amfibibia na reptilia wanaopatikana msitu wa Kakamega*. National Museums of Kenya and University of Mainz, Nairobi & Mainz, Namibia, Germany. 1-112.
- Loveridge A (1955) On Amphibia Salientia from the Ivory Coast. *Revue suisse de Zoologie* 62: 129-150.
- Loveridge A (1956) VI. Amphibiens. In: *Le Parc National de Niokolo-Koba. Mémoires de l'Institut fondamental d'Afrique noires* 48: 163-166.
- Magurran AE & McGill BJ (2011) *Biological Diversity – frontiers in measurement and assessment*. Oxford University Press, Oxford, UK. 1-364.
- Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd., Oxford, UK. 1-256.
- Maley J (1996) The African rainforest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proceedings of the Royal Society of Edinburgh* 104B: 31-73.
- Malonza PK, Wasonga VD, Muchai V, Rotich D, Bwong BA (2006) Diversity and Biogeography of Herpetofauna of the Tana River Primate National Reserve, Kenya. *Journal of East African Natural History* 95: 95-109.
- Manni F, Guérard E & Heyer E (2004) Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. *Human Biology* 76: 173-190.
- Marchant R (1990) The robustness of classification and ordination techniques applied to macroinvertebrate communities from the La Trobe River, Victoria. *Australian Journal of Marine and Freshwater Research* 41: 493-504.
- Marsh D & Trenham PC (2001) Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15: 40-49.



- Mayaux P, Bartholomé E, Fritz S & Belward A (2004) A new land-cover map of Africa for the year 2000. *Journal of Biogeography* 31: 861-877.
- Mayaux P, Holgren P, Achard F, Eva H, Stibig H-J & Branthomme A (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society B* 360: 373-384.
- Mayaux P, Pekel J-F, Desclée B, Donnay F, Lupi A, Achard F, Clerici M, Bodart C, Brink A, Nasi R & Belward A (2013) State and evolution of the African rainforests between 1990 and 2010. *Philosophical Transactions of the Royal Society B* 368: 20120300.
- Mayr E & O'Hara RJ (1986) The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution* 40: 55-67.
- Mazzoni R, Cunningham AA, Daszak P, Apolo A, Perdomo E & Speranza G (2003) Emerging pathogen of wild amphibians in frogs (*Rana catesbeiana*) farmed for international trade. *Emerging Infectious Diseases* 9: 995-998.
- McCune B & Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach, USA. 1-304.
- McDonald KR & Alford RA (1999) A review of declining frogs in northern Queensland. In: Campbell A (ed). *Declines and disappearances of Australian frogs*. Environment Australia, Canberra, Australia. 14-22.
- McKnight MW, White PS, McDonald RI, Lamoreux JF, Sechrest W, Ridgley RS & Stuart SN (2007) Putting beta-diversity on the map: broad scale congruence and coincidence in the extremes. *PLoS Biology* 5: e272.
- Mendez D, Speare R & Cunningham AA (1999) In: Speare R, Berger L. (2000) Global distribution of chytridiomycosis in amphibians. <http://www.jcu.edu.au/school/phtm/PHTM/frogs/chyglob.htm> (last accessed: 26 April 2011).
- Menegon M & Salvidio S (2005) Amphibian and Reptile diversity in the southern Udzungwa Scarp Forest Reserve, south-eastern Tanzania. In: Huber BA, Sinclair BJ & Lampe KH (eds) *African Biodiversity: Molecules, Organisms, Ecosystems*. Springer Science & Media Inc., New York, USA. 205-212.
- Mertens R (1938) Herpetologische Ergebnisse einer Reise nach Kamerun. *Abhandlungen der senckenbergisch naturforschenden Gesellschaft* 442, 1-52.
- Mertens R (1940) Zur Herpetologie Kameruns und Deutsch-Ostafrikas. *Zoologischer Anzeiger* 131: 239-250.
- Miles MA, Thomson AG, Walters GW (1978) Amphibians and reptiles from the vicinity of Boughari, Casamance (Senegal), and the Gambia. *Bulletin de l'Institut fondamental d'Afrique noire Sér. A* 40: 437-456.
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermaier CG, Lamoreux J & Da Fonseca GAB (2004) Hotspots revisited. Conservation International, Washington DC, USA. 1-392.
- Mohneke M, Onadeko AB & Rödel M-O (2009) Exploitation of frogs - a review with a focus on West Africa. *Salamandra* 45: 193-202.
- Mohneke M, Onadeko AB, Hirschfeld M & Rödel M-O (2010) Dried or fried: amphibians in local and regional food markets in West Africa. *TRAFFIC Bulletin* 22: 117-128.
- Moilanen A (2007) Landscape Zonation, benefit functions and target-based planning. *Unifying reserve selection strategies*. *Biological Conservation* 134: 571-579.
- Moilanen A, Franco AMA, Early R, Fox R, Wintle B & Thomas CD (2005) Prioritising multiple use landscapes for conservation: methods for large multi species planning problems. *Proceedings of the Royal Society B*: 272: 1885-1891.
- Moilanen A, Wilson KA & Possingham HP (2009) Spatial conservation prioritization. Oxford University Press, Oxford, UK. 1-304.
- Monmonier MS (1973) Maximum difference barriers: an alternative numerical regularization method. *Geographical Analysis* 5: 245-261.
- Moodley Y & Bruford MW (2007) Molecular biogeography: towards an integrated framework for conserving Pan-African biodiversity. *PLoS ONE* 2: e454.
- Mora C, Tittensor DP, Adl S, Simpson AGB & Worm B (2011) How many species are there on earth and in the ocean? *PLoS Biology* 9: e1001127.
- Moritz C, Patton JL, Schneider CJ & Smith TB (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology, Evolution, and Systematics* 31: 533-563.
- Morley RJ (2000) Origin and evolution of tropical rainforests. John Wiley & Sons, Chichester, UK. 1-362.
- Morrison C & Hero J-M (2003). Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology* 72: 270-279.
- Mouchot M, Guilhaumon F, Villéger S, Mason NWH, Tomasini J-A & Mouillot D (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117: 794-800.



- Mountford MD (1962) An index of similarity and its application to classification problems. In: Murphy PW (ed) Progress in soil zoology. Butterworth, London, UK. 43-50.
- Murray BR, Fonseca CR & Westoby M (1998) The macroecology of Australian frogs. *Journal of Animal Ecology* 67: 567-579.
- Murray K, Skerratt L, Marantelli G, Berger L, Hunter D, Mahony M & Hines H (2011) Hygiene protocols for the control of diseases in Australian frogs. A report for the Australian Government Department of Sustainability, Environment, Water, Population and Communities, Canberra. 1-26.
- Murray K, Skerratt LF, Speare R & McCallum H (2009) Detecting the impact and dynamics of disease in species threatened by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*. *Conservation Biology* 23: 1242-1252.
- Murray KA & Skerratt LF (2012) Predicting wild hosts for amphibian chytridiomycosis: integrating host life-history traits with pathogen environmental requirements. *Human and Ecological Risk Assessment* 18: 200-224.
- Murray KA, Retallick RWR, Puschendorf R, Skerratt LF, Rosauer D, McCallum HI, Berger L, Speare R & VanDerWal J (2011) Assessing spatial patterns of disease risk to biodiversity: implications for the management of the amphibian pathogen, *Batrachochytrium dendrobatidis*. *Journal of Applied Ecology* 48: 163-173.
- Muths E, Corn PS, Pessier AP & Green DE (2003) Evidence for disease-related amphibian decline in Colorado. *Biological Conservation* 110: 357-365.
- Myers N (1988) Threatened biotas: "hot spots" in tropical forests. *The Environmentalist* 8: 187-208.
- Myers N (1990) The biodiversity challenge: expanded hotspots analysis. *The Environmentalist* 10: 243-256.
- Myers N, Mittermeier RA, Mittermeier CG, DaFonseca GAB & Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853-845.
- Nago SGA, Grell O, Sinsin B & Rödel M-O (2006) The amphibian fauna of the Pendjari National Park and surroundings, northern Benin. *Salamandra* 42: 93-108.
- Nichol JE (1999) Geomorphological evidence and Pleistocene refugia in Africa. *The Geographical Journal* 165 79-89.
- Nicolas V, Brya J, Akpatou B, Konecny A, Lecompte E, Colyn M, Lalis A, Couloux A, Denys C & Granjon L (2008) Comparative phylogeography of two sibling species of forest-dwelling rodent (*Praomys rostratus* and *P. tullbergi*) in West Africa: different reactions to past forest fragmentation. *Molecular Ecology* 17: 5118-5134.
- Norris K, Asase A, Collen B, Gockowski J, Mason J, Phalan B & Wade A (2010) Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests. *Biological Conservation* 143: 2341-2350.
- Nylander JAA (2002) MrModeltest 1.1b, Uppsala, Sweden.
- Oates JF, Bergl RA & Linder JM (2004) Africa's Gulf of Guinea forests: biodiversity patterns and conservation priorities. *Advances in Applied Biodiversity Science*, No. 6, Conservation International, Washington DC, USA. 1-89.
- Ofori-Boateng C, Oduro W, Hillers A, Norris K, Oppong SK, Adum GB & Rödel M-O (2012) Differences in the effects of selective logging on amphibian assemblages in three West African forest types. *Biotropica* 45: 94-101.
- Oksanen J, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH & Wagner H (2013) vegan: Community Ecology Package, Version 2.0-10. <http://CRAN.R-project.org/package=vegan> (last accessed December 2013).
- Oksanen, J. (2008) The vegan package, version 1.15-2. <http://CRAN.R-project.org/package=vegan> (last accessed December 2008)
- Olalla-Tárraga MA, Diniz-Filho AF, Bastos RP & Rodríguez MA (2009) Geographic body size gradients in tropical regions: water deficit and anuran body size in the Brazilian Cerrado. *Ecography* 32: 581-590.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CL, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P & Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. *BioScience* 51: 933-938.
- Onadeko AB & Rödel M-O (2009) Anuran surveys in south-western Nigeria. *Salamandra* 45: 1-14.
- Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding T-S, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ & Owens IPF (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436: 1016-1019.
- Ortega-Huerta MA & Peterson AT (2008) Modeling ecological niches and predicting geographic distributions: a test of six presence-only methods. *Revista Mexicana de Biodiversidad* 79: 205-216.
- Padial JM & de la Riva I (2004) Annotated checklist of the amphibians of Mauritania (West Africa). *Revista Española de Herpetología* 18: 89-99.
- Palo JU, Schmeller DS, Laurila A, Primmer CR, Kuzmin SK & Merilä J (2004) High degree of population subdivision in a widespread amphibian. *Molecular Ecology* 13: 2631-3644.



- Palumbi S, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR, version 2. Honolulu, Hawaii.
- Palumbi SR (1991) Nucleic Acids II: the Polymerase Chain Reaction. In: Hillis DM, Moritz C & Mable BK (eds) Molecular Systematics. 2nd ed, Sinauer Associates, Sunderland, USA. 205-247.
- Parker HW (1931) Some new and rare frogs from West Africa. The Annals and Magazine of Natural History 7: 492-498.
- Parker HW (1936) Amphibians from Liberia and the Gold Coast. Zoologische Mededelingen 19: 87-102.
- Parker JM, Mikaelian I, Hahn N & Diggs HE (2002) Clinical diagnosis and treatment of epidermal Chytridiomycosis in African Clawed Frogs (*Xenopus tropicalis*). Comparative Medicine 52: 265-268.
- Pauwels OSG & Rödel M-O (2007) Amphibians and national parks in Gabon, western Central Africa. Herpetozoa 19: 135-148.
- Pearson RG & Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12: 361-371.
- Penner J, Adum GB, McElroy MT, Doherty-Bone T, Hirschfeld M, Sandberger L, Weldon C, Cunningham AA, Ohst T, Wombwell E, Portik DM, Reid D, Hillers A, Ofori-Boateng C, Oduro W, Plötner J, Ohler A, Leaché AD & Rödel M-O (2013) West Africa – A safe haven for frogs? A sub-continental assessment of the chytrid fungus (*Batrachochytrium dendrobatidis*). PLoS ONE 8: e56236.
- Penner J, Wegmann M, Hillers A, Schmidt M & Rödel M-O (2011) A hotspot revisited - a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077-1088.
- Perret J-L (1966) Les amphibiens du Cameroun. Zoologische Jahrbücher (Systematik) 8: 289-464.
- Perret J-L (1988) Les espèces de *Phrynobatrachus* (Anura, Ranidae) à éperon palpébral. Archives des Sciences Genève 41: 275-294.
- Peters W (1875) Über die von Hrn. Professor Dr. R. Buchholz in Westafrika gesammelten Amphibien. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin März: 196–212 + 3 plates.
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M & Araújo MB (2011) Ecological niches and geographic distributions. Monographs in Population Biology 49: 1-314.
- Phillips SJ & Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecology 89: 161-175.
- Phillips SJ, Anderson RP & Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259.
- Phillips SJ, Dudík M & Schapire RE (2004) A maximum entropy approach to species distribution modeling. In: Brodley C (ed) Proceedings of the Twenty-First International Conference on Machine Learning. ACM Press, New York, USA. 655-662.
- Phillott AD, Speare R, Hines HB, Skerratt LF, Meyer E, McDonald KR, Cashins SD, Mendez D & Berger L (2010) Minimising exposure of amphibians to pathogens during field studies. Diseases of Aquatic Organisms 92: 175-185.
- Pienaar U de V, Passmore NI & Carruthers VC (1963) The frogs of Kruger National Park. National Parks Board of South Africa, Pretoria. 1-91.
- Pigot AL, Owens IPF & Orme CDL (2012) Speciation and extinction drive the appearance of directional range size evolution in phylogenies and the fossil record. PLoS Biology 10: e1001260.
- Pimm SL, Russell GJ, Gittleman JL & Brooks TM (1995) Science 269: 347-350.
- Piotrowski JS, Annis SL & Longcore JE (2004) Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. Mycologia 96: 9-15.
- Plath M, Solbach M & Herrmann H-W (2004) Anuran habitat selection and temporal partitioning in a montane and submontane rainforest on Southwestern Cameroon - first results. Salamandra 40: 239-260.
- Plath M, Solbach M & Herrmann H-W (2004) Anuran habitat selection and temporal partitioning in a montane and submontane rainforest in Southwestern Cameroon - first results. Salamandra 40: 239-260.
- Poorter L, Bongers F, Kouamé FN & Hawthorne WD (2004) Biodiversity of West African Forests. An ecological atlas of woody plant species. CABI Publishing, Wallington. 1-521.
- Posada D & Crandall KA (1998) MODELTEST: testing the model of DNA substitution. Bioinformatics 14: 817-818.
- Poynton JC (1962) Zoogeography of eastern Africa: an outline based on anuran distribution. Nature 4835: 1217-1219.
- Poynton JC (1995) The "arid corridor" distribution in Africa: a search for instances among amphibians. Madoqua 19: 45-48.



- Poynton JC (1999) Distribution of amphibians in sub-Saharan Africa, Madagascar, and Seychelles. In: Duellman WE (ed) Patterns of distribution of amphibians, a global perspective. John Hopkins University Press, Baltimore, USA. 483-539.
- Poynton JC (2000) Amphibians. In: Burgess ND & Clarke GP (eds) *The coastal forests of eastern Africa*. IUCN, Gland, Switzerland. 201-210.
- Poynton JC, Loader SP, Sherratt E & Clarke BT (2007) Amphibian diversity in East African biodiversity hotspots: altitudinal and latitudinal patterns. *Biodiversity and Conservation* 16: 1103-1118.
- Puschendorf R, Carnaval AC, VanDerWal J, Zumbado-Ulate H, Chaves G, Bolaños F & Alford RA (2009) Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica: proposing climatic refuges as a conservation tool. *Diversity and Distributions* 15: 401-408.
- Pyron RA & Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61: 543-583.
- R 2.9.0 (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/> (last accessed December 2013).
- Rachowicz LJ, Knapp RA, Morgan JAT, Stice MJ, Vredenburg VT, Parker JM & Briggs CJ (2006) Emerging infectious disease as a proximate cause of amphibian mass mortality. *Ecology* 87: 1671-1683.
- Raup D & Crick RE (1979) Measurement of faunal similarity in paleontology. *Journal of Paleontology* 53: 1213-1227.
- Raxworthy CJ & Attuquayefio DK (2000) Herpetofaunal communities at Muni Lagoon in Ghana. *Biodiversity and Conservation* 9: 501-510.
- Razetti E & Msuya C A (2002) *Field guide to the amphibians and reptiles of Arusha National Park (Tanzania)*. Publ. Ed. Negri Istituto, Oikos, Varese, Italy. 1-85.
- Reeder NMM, Chang TL, Vredenburg VT & Blackburn DC (2011) Survey of the chytrid fungus *Batrachochytrium dendrobatidis* from montane and lowland frogs in eastern Nigeria. *Herpetology Notes* 4: 83-86.
- Reeder TW (2003) A phylogeny of the Australian *Sphenomorphus* group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (*Tribolonotus*): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. *Molecular Phylogenetics and Evolution* 27: 384-397.
- Renaud JM & Stevens ED (1983) A comparison between field habitats and contractile performance of frog and toad sartorius muscle. *Journal of Comparative Physiology* 151: 127-131.
- Ribas L, Li M-S, Doddington BJ, Robert J, Seidel JA, Kroll JS, Zimmermann LB, Grassley NC, Garner TWJ & Fisher MC (2009) Expression profiling the temperature-dependent amphibian response to infection by *Batrachochytrium dendrobatidis*. *PLoS One* 4: e8408.
- Rizopoulos D (2006) ltm: An R package for latent variable modelling and item response theory analyses. *Journal of Statistical Software* 17: 1-25.
- Roberts TR (1975) Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnean Society* 57: 249-319.
- Rödder D, Kielgast J & Lötters S (2010) Future potential distribution of the emerging amphibian chytrid fungus under anthropogenic climate change. *Diseases of Aquatic Organisms* 92: 201-207.
- Rödder D, Kielgast J, Bielby J, Schmidlein S, Bosch J, Garner TWJ, Veith M, Walker S, Fisher MC & Lötters S (2009) Global amphibian extinction risk assessment for the Panzootic chytrid fungus. *Diversity* 1: 52-66.
- Rödder D, Veith M & Lötters S (2008) Environmental gradients explaining the prevalence and intensity of infection with the amphibian chytrid fungus: the host's perspective. *Animal Conservation* 11: 513-517.
- Rödel M-O & Agyei AC (2003) Amphibians of the Togo-Volta highlands, eastern Ghana. *Salamandra* 39: 207-234.
- Rödel M-O & Bangoura M (2004) Rapid survey of amphibians and reptiles in the Forêt Classée du Pic de Fon, Guinée / Évaluation rapide des amphibiens et des reptiles dans la Forêt Classée du Pic de Fon, Guinée. In: McCullough J (ed) A rapid biological assessment of the Forêt Classée du Pic de Fon, Simandou Range, South-eastern Republic of Guinea / Une évaluation biologique rapide de la Forêt Classée du Pi de Fon, chaîne du Simandou, Guinée. RAP Bulletin of Biological Assessment 35, Conservation International, Washington DC, USA. 51-60, 151-164, 232-237.
- Rödel M-O & Bangoura MA (2004) A conservation assessment of amphibians in the Forêt Classée du Pic de Fon, Simandou Range, southeastern Republic of Guinea, with the description of a new *Amnirana* species (Amphibia Anura Ranidae). *Tropical Zoology* 17: 201-232.



- Rödel M-O & Bangoura MA (2006) Un inventaire herpétologique de trois forêts classées dans le sud-est de la République de Guinée / A herpetological survey of Déré, Diécké and Mt. Béro classified forests, southeastern Guinea. In: Wright HE, McCullough J, Alonso LE & Diallo MS (eds) Une évaluation biologique rapide de trois forêts classées du sud-est de la Guinée / A rapid biological assessment of three classified forests in southeastern Guinea. RAP Bulletin of Biological Assessment 40, Conservation International, Washington DC, USA. 53-58, 153-158, 229-235.
- Rödel M-O & Branch WR (2002) Herpetological survey of the Haute Dodo and Cavally forests, western Ivory Coast, Part I: Amphibians. *Salamandra* 38: 245-268.
- Rödel M-O & Branch WR (2005) Inventaire herpétologique des forêts de la Haute Dodo et du Cavally à l'ouest de la Côte d'Ivoire / Herpetological survey of the Haute Dodo and Cavally forests, western Côte d'Ivoire. In: Alonso LE, Lauginie F & Rondeau G (eds). Une évaluation biologique de deux forêts classées du sud-ouest de la Côte d'Ivoire / A rapid biological assessment of two classified forests in south-western Côte d'Ivoire. RAP Bulletin of Biological Assessment 34, Conservation International, Washington DC, USA. 57-66, 67-74, 154-161.
- Rödel M-O & Ernst R (2002a) A new reproductive mode for the genus *Phrynobatrachus*: *Phrynobatrachus alticola* has nonfeeding, nonhatching tadpoles. *Journal of Herpetology* 36: 121-125.
- Rödel M-O & Ernst R (2002b) A new *Phrynobatrachus* from the Upper Guinean rain forest, West Africa, including a description of a new reproductive mode for the genus. *Journal of Herpetology* 36: 561-571.
- Rödel M-O & Ernst R (2003) The amphibians of Marahoué and Mont Péko National Parks, Ivory Coast. *Herpetozoa* 16: 23-39.
- Rödel M-O & Spieler M (2000) Trilingual keys to the savannah anurans of the Comoé National Park, Ivory Coast. *Stuttgarter Beiträge zur Naturkunde Serie A* 620: 1-31.
- Rödel M-O (1996) Amphibien der westafrikanischen Savanne. Edition Chimaira, Frankfurt/M, Germany. 1-283 + 8 plates.
- Rödel M-O (1998) Kaulquappengesellschaften ephemerer Savannengewässer in Westafrika. Edition Chimaira, Frankfurt/M, Germany. 1-195.
- Rödel M-O (2000) Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna. Edition Chimaira, Frankfurt/M, Germany. 1-335.
- Rödel M-O (2003) The amphibians of Mont Sangbé National Park, Ivory Coast. *Salamandra* 39: 91-110.
- Rödel M-O, Bangoura MA & Böhme W (2004) The amphibians of south-eastern Republic of Guinea (Amphibia: Gymnophiona, Anura). *Herpetozoa* 17: 99-118.
- Rödel M-O, Boateng CO, Penner J & Hillers A (2009) A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa. *Zootaxa* 1970: 52-63.
- Rödel M-O, Brede C, Schiefenhövel P, Penner J, Sinsin B & Nago SGA (2007) The amphibians of the Lokoli Forest, a permanently inundated rainforest in the Dahomey Gap, Benin. *Salamandra* 43: 231-238.
- Rödel M-O, Doumbia J, Johnson AT & Hillers A (2009c) A new small *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Liberian part of Mount Nimba, West Africa. *Zootaxa* 2302: 19-30.
- Rödel M-O, Gil M, Agyei AC, Leaché AD, Diaz RE, Fujita MK & Ernst R (2005b) The amphibians of the forested parts of south-western Ghana. *Salamandra* 41: 107-127.
- Rödel M-O, Kosuch J, Grafe TU, Boistel R, Assemian NE, Kouamé NG, Tohé B, Gourène G, Perret J-L, Henle K, Tafforeau P, Pollet N & Veith M (2009b) A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). *Zootaxa* 2044: 23-45.
- Rödel M-O, Kosuch J, Kouamé NG, Ernst R & Veith M (2005a) *Phrynobatrachus alticola* Guibé & Lamotte, 1961 is a junior synonym of *Phrynobatrachus tokba* (Chabanaud, 1921). *African Journal of Herpetology* 54: 93-98.
- Rödel M-O, Sandberger L, Doumbia J & Hillers A (2009d) Revalidation of *Phrynobatrachus maculiventris* Guibé & Lamotte, 1958 and description of its aposematic coloured tadpole. *African Journal of Herpetology* 58: 15-27.
- Roelants K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Moriau L & Bossuyt F (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences* 104: 887-892.
- Ron SR (2005) Predicting the distribution of the amphibian pathogen *Batrachochytrium dendrobatidis* in the New World. *Biotropica* 37: 209-221.
- Rondinini C, Chiozza F & Boitani L (2006) High human density in the irreplaceable sites for African vertebrates conservation. *Biological Conservation* 133: 358-363.
- Rondinini C, Di Marco M, Chiozza F, Santulli G, Baisero D, Visconti P, Hoffmann M, Schipper J, Stuart SN, Tognelli MF, Amori G, Falcucci A, Maiorano L & Boitani L (2011) Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B* 366: 2633-2641.



- Rothermel BB & Semlitsch RD (2002) An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* 16: 1324-1332.
- Safi K, Armour-Marshall K, Baillie JEM & Isaac NJB (2013) Global patterns of evolutionary distinct and globally endangered amphibians and mammals. *PLoS ONE* 8: e63582.
- Sandberger L, Feldhaar H, Lampert KP, Lamatsch DK & Rödel M-O (2010) Small, specialised and highly mobile? The tree-hole breeding frog, *Phrynobatrachus guineensis*, lacks fine-scale population structure. *African Journal of Herpetology* 59: 79-94.
- Sandberger L, Hillers A, Doumbia J, Loua N-S, Brede C & Rödel M-O (2010) Rediscovery of the Liberian Nimba toad, *Nimbaphrynoides liberiensis* (Xavier, 1978) (Amphibia: Anura: Bufonidae), and reassessment of its taxonomic status. *Zootaxa* 2355: 56-68.
- Sanders HL (1968) Marine benthic diversity: a comparative study. *The American Naturalist* 925: 243-282.
- Schiøtz A (1963) The amphibians of Nigeria. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 125: 1-92 + 4 plates.
- Schiøtz A (1964a) A preliminary list of amphibians collected in Ghana. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 127: 1-17.
- Schiøtz A (1964b) A preliminary list of amphibians collected in Sierra Leone. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 127: 19-33 + 1 plate
- Schiøtz A (1964b) The voices of some West African amphibians. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 127: 35-83.
- Schiøtz A (1966) On a collection of amphibia from Nigeria. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 129: 43-48 + 3 plates.
- Schiøtz A (1967) The treefrogs (Rhacophoridae) of West Africa. *Spolia Zoologica Musei Hauniensis* 25: 1-346.
- Schiøtz A (1971) The superspecies *Hyperolius viridiflavus* (Anura). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 134: 21-76.
- Schiøtz A (1975) The treefrogs of Eastern Africa. *Steenstrupia*, Copenhagen, Denmark. 1-232.
- Schiøtz A (1981) The Amphibia in the forested basement hills of Tanzania: a biogeographical indicator group. *African Journal of Ecology* 19: 205-207.
- Schiøtz A (1999) Treefrogs of Africa. Edition Chimaira, Frankfurt/M, Germany. 1-350.
- Schiøtz A (2007) Zoogeography of the treefrogs in Africa's tropical forests. *Alytes* 25: 1-37.
- Schloegel LM, Ferreira CM, James TY, Hipolito M, Longcore JE, Hyatt AD, Yabsley M, Martins AMCRPF, Mazzoni R, Davies AJ & Daszak P (2010) The North American bullfrog as a reservoir for the spread of *Batrachochytrium dendrobatidis* in Brazil. *Animal Conservation* 13: 53-61.
- Schloegel LM, Picco AM, Kilpatrick AM, Davies AJ, Hyatt AD & Daszak P (2009) Magnitude of the US trade in amphibians and presence of *Batrachochytrium dendrobatidis* and ranavirus infection in imported North American bullfrogs (*Rana catesbeiana*). *Biological Conservation* 142: 1420-1426.
- Schloegel LM, Toledo LF, Longcore JE, Greenspan SE & Vieira CA (2012) Novel, panzootic and hybrid genotypes of amphibian chytridiomycosis associated with the bullfrog trade. *Molecular Ecology* 21: 5162-5177.
- Schmidt BR, Furrer S, Kwet A, Lötters S, Rödder D, Szatecsny M, Tobler U & Zumbach S (2009) Desinfektion als Maßnahme gegen die Verbreitung der Chytridiomykose bei Amphibien. *Zeitschrift für Feldherpetologie*, Supplement 15: 229-241.
- Schmitz A, Euskirchen O, & Böhme W (1999) Zur Herpetofauna einer montanen Regenwaldregion in SW-Kamerun (Mt. Kupe und Bakossi-Bergland), 1.: Einleitung Bufonidae und Hyperoliidae. *Herpetofauna* 21: 5-17.
- Schorr G (2003) Die Amphibiengemeinschaften auf Inselbergen im Taï-Nationalpark, Côte d'Ivoire, Westafrika - Gemeinschaftsökologische und inselbiogeographische Aspekte. Unpublished Diploma Thesis, University of Würzburg, Germany. 1-93.
- Scotese CR (2001) PALEOMAP Project. Version 1 (2010). <http://www.scotese.com> (last accessed on 11 November 2013).
- Segniagbeto GH, Bowessidjaou JE, Dubois A & Ohler A (2007) Les amphibiens du Togo: état actuel des connaissances. *Alytes* 24: 72-90.
- Semlitsch RD (1981) Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management* 72: 260-267.
- Seymour CL, De Klerk HM, Channing A & Crowe TM (2001) The biogeography of the Anura of sub-equatorial Africa and the prioritisation of areas for their conservation. *Biodiversity and Conservation* 10: 2045-2076.



- Shepard RB (1984) The logseries distribution and Mountford's similarity index as a basis for the study of stream benthic community structure. *Freshwater Biology* 14: 53-71.
- Shriner SA, Wilson KR & Flather CH (2006) Reserve networks based on richness hotspots and representation with scale. *Ecological Applications* 16: 1660-1673.
- Simberloff D (1972) Properties of the rarefaction diversity measurement. *The American Naturalist* 106: 414-418.
- Simbotwe MP & Friend GR (1985) Comparison of the herpetofaunas of tropical wetland habitats from Lochinvar National Park, Zambia and Kakadu National Park, Australia. *Proceedings of the Ecological Society of Australia* 14: 141-151.
- Sinsch U (1990) Migration and orientation in anuran amphibians. *Ethology, Ecology and Evolution* 2: 65-69.
- Skerratt LF, Berger L, Speare R, Cashins S, McDonald KR, Phillott AD, Hines HB & Kenyon N (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth* 4: 125-134.
- Skerratt LF, McDonald KR, Hines HB, Berger L, Mendez D, Phillott AD, Cashins SD, Muray KA & Speare R (2010) Applications of the survey protocol for chytridiomycosis to Queensland, Australia. *Diseases of Aquatic Organisms* 92: 117-129.
- Skerratt LF, Mendez D, McDonald KR, Garland S, Livingstone J, Berger L & Speare R (2011) Validation of diagnostic tests in wildlife: the case of chytridiomycosis in wild amphibians. *Journal of Herpetology* 45: 444-450.
- Slatyer RA, Hirst M & Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecology Letters* 16: 1104-1114.
- Smith MA & Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28: 110-128.
- SMUWC (2001) Talking about Usangu: Annex 1 Baseline 2001. SMUWC Technical Report, Iringa.
- Sneath PHA & Sokal RR (1973) Numerical taxonomy. W.H. Freeman & Company, San Francisco, USA. 1-573.
- Sosef MSM (1994) Refuge begonias: taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa. Wageningen Agricultural University Papers, Studies in Begoniaceae 5: 1-306.
- Soto-Azat C, Clarke BT, Fisher MC, Walker SF & Cunningham AA (2009) Noninvasive sampling methods for the detection of *Batrachochytrium dendrobatidis* in archived amphibians. *Diseases of Aquatic Organisms* 84: 163-166.
- Soto-Azat C, Clarke BT, Poynton JC & Cunningham AA (2010) Widespread historical presence of *Batrachochytrium dendrobatidis* in African pipid frogs. *Diversity and Distributions* 16: 126-131.
- Spieler M & Linsenmair KE (1998) Migration and diurnal shelter in a ranid frog from a West African savannah: a telemetric study. *Amphibia-Reptilia* 19: 43-64.
- Spieler M (1997) Anpassungen westafrikanischer Froschlurche an Trockenstreß und Räuberdruck in einer westafrikanischen Savanne. *Salamandra* 33: 133-152.
- St-Amour V, Wong WM, Garner TWJ & Lesbarrères D (2008) Anthropogenic influence on prevalence of 2 amphibian pathogens. *Emerging Infectious Diseases* 14: 1175-1176.
- Stockwell MP, Culow J & Mahony MJ (2010) Host species determines whether infection load increases beyond disease-causing thresholds following exposure to the amphibian chytrid fungus. *Animal Conservation* 13, Supplement 1: 62-71.
- Stuart S, Hoffmann M, Chanson J, Cox N, Berridge R, Ramani P & Young B (2008) Threatened amphibians of the world. Lynx Edition, Barcelona, Spain. 1-758.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL & Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783-1786.
- Swofford DL (2001) Paup*: phylogenetic analysis using parsimony (and other methods), version 4.06b. Sinauer Associates, Sunderland/Massachusetts.
- Swofford DL (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Szymura JM & Barton NH (1991) The genetic structure of the hybrid zone between the fire-bellied toads *Bombina bombina* and *B. variegata*: comparisons between transects and between loci. *Evolution* 45: 237-261.
- Thuiller W, Broennimann O, Hughes G, Alkemade JRM, Midgley GF & Corsi F (2006) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology* 12: 424-440.
- Tinoco BA, Astudillo PX, Latta SC & Graham CH (2009) Distribution, ecology and conservation of an endangered Andean hummingbird: the Violet-throated Metaltail (*Metallura baroni*). *Bird Conservation International* 19: 63-76.



- Tittensor DP, Baco AR, Brewin PE, Clark MR, Consalvey M, Hall-Spencer J, Rowden AA, Schlacher T, Stocks KI & Rogers AD (2009) Predicting global habitat suitability for stony corals on seamounts. *Journal of Biogeography* 36: 1111-1128.
- Tuomisto H (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33: 2-22.
- Tuomisto H (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33: 23-45.
- Tuomisto H (2010c) A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164: 853-860.
- Tuomisto H (2012) An updated consumer's guide to evenness and related indices. *Oikos* 121: 1203-1218.
- Udvardy MDF (1975) A classification of the biogeographical provinces of the world. IUCN Occasional Paper 18: 1-50.
- Underwood EC, Shaw MR, Wilson KA, Kareiva P, Klausmeyer KR, McBride MF, Bode M, Morrison SA, Hoekstra JM & Possingham HP (2008) Protecting biodiversity when money matters: maximizing return on investment. *PLoS ONE* 3: e1515.
- Uyeda JC, Drewes RC & Zimkus BM (2007) The California Academy of Sciences Gulf of Guinea Expeditions (2001, 2006) VI. A new species of *Phrynobatrachus* from the Gulf of Guinea Islands and a reanalysis of *Phrynobatrachus dispar* and *P. feae* (Anura: Phrynobatrachidea). *Proceedings of the California Academy of Sciences* 58: 367-385.
- Van Sluys M, Kriger KM, Phillott AD, Campbell R, Skerratt LF & Hero JM (2008) Storage of samples at high temperatures reduces the amount of amphibian chytrid fungus *Batrachochytrium dendrobatidis* DNA detectable by PCR assay. *Diseases of Aquatic Organisms* 81: 93-97.
- Veith M (2004) Subproject E08 Biodiversity change in frogs from eastern Africa: global, regional or local causes? In: BIOTA East Africa - Final Report Phase I (2001-2004). 101-110.
- Veith M, Kosuch J, Rödel M-O, Hillers A, Schmitz A, Burger M & Lötters S (2009) Multiple evolution of sexual dichromatism in African reed frogs. *Molecular Phylogenetics and Evolution* 51: 388-393.
- Vences M, Thomas M, Bonett RM & Vieites DR (2005a) Deciphering amphibian diversity through DNA barcoding: changes and challenges. *Philosophical Transactions of the Royal Society B* 360: 1859-1868.
- Vences M, Thomas M, van der Meijden A, Chiari Y & Vieites DR (2005b) Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Frontiers in Zoology* 2: 5
- Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F & Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences* 106: 19715-19722.
- Voelker G, Outlaw RK & Bowie RCK (2010) Pliocene forest dynamics as a primary driver of African bird speciation. *Global Ecology and Biogeography* 19: 111-121.
- Vonesh JR (1998) The Amphibians and Reptiles of Kibale Forest, Uganda: herpetofaunal survey and ecological study of the forest floor litter community. Unpublished MSc thesis, Department of Zoology, University of Florida, Gainesville, Florida. 1-111.
- Vonesh JR (2001) Natural history and biogeography of the amphibians and reptiles of Kibale National Park, Uganda. *Contemporary Herpetology* 4: 1-26.
- Vredenburg VT, du Preez L, Raharivololoniaina L, Vieites DR, Vences M, Weldon C (2012) A molecular survey across Madagascar does not yield positive records of the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. *Herpetology Notes* 5: 507-517.
- Vuattoux R (1968) Le peuplement du palmier rônier (*Borassus aethiopum*) d'une savane de Côte d'Ivoire. *Annales de l'Université d'Abidjan, Sér. E* 1: 1-138.
- Wagner P, Köhler J, Schmitz A & Böhme W (2008) The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. *Journal of Biogeography* 35: 1349-1361.
- Wake DB (2012) Facing extinction in real time. *Science* 335: 1052-1053.
- Waldman B, van de Wolfshaar KE, Klena JD, Andjic V, Bishop PJ, Norman RJ de B (2001) Chytridiomycosis in New Zealand frogs. *Surveillance* 28: 9-11.
- Walker RB (1968) The amphibians of Zaria, in the northern Guinea savannah, Nigeria. *Copeia* 1968: 164-167.
- Wanger TC (2005) Amphibians of Kiang West National Park, The Gambia. *Salamandra* 41: 27-33.
- Warman LD, Sinclair ARE, Scudder GGE, Klinkenberg B & Pressey RL (2004) Sensitivity of systematic reserve selection to decisions about scale, biological data, and targets: case study from southern British Columbia. *Conservation Biology* 18: 655-666.
- Wasonga DV, Bakele A, Lötters S & Balakrishnan M (2007) Amphibian abundance and diversity in Meru National Park, Kenya. *African Journal of Ecology* 45: 55-61.



- Webb R, Mendez D, Berger L & Speare R (2007) Additional disinfectants effective against the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. *Diseases of Aquatic Organisms* 74: 13-16.
- Wegmann M (2009) Analyse von räumlichen Landschaftsmustern und deren Determinanten mittels Fernerkundungsdaten am Beispiel von Regenwaldfragmenten in Westafrika. Unpublished PhD Thesis, University of Würzburg, Germany. 1-233.
- Weldon C & du Preez LH (2004) Decline of Kihansi spray toad, *Nectophrynoides asperginis*, from the Udzungwa mountains, Tanzania. *Froglog* 62: 2-3.
- Weldon C & Fisher MC (2011) The effect of trade-mediated spread of amphibian chytrid on amphibian conservation. In: IOM (Institute of Medicine) (ed) *Fungal diseases: An emerging challenge to human, animal, and plant health*. The National Academies Press, Washington DC, USA. 355-367.
- Weldon C (2005) Chytridiomycosis, an emerging infectious disease of amphibians in South Africa. PhD Thesis. Potchefstroom, North-West University, South Africa. 1-213.
- Weldon C, de Villiers L & du Preez LH (2007) Quantification of the trade in *Xenopus laevis* from South Africa, with implications for biodiversity conservation. *African Journal of Herpetology* 56: 77-83.
- Weldon C, du Preez L & Vences M (2008) Lack of detection of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in Madagascar. In: Andreone F (ed) *A Conservation Strategy for the Amphibians of Madagascar*. Monografie XLV Torino, Museo Regionale di Scienze Naturali, Trento, Italy. 95-106.
- Weldon C, du Preez LH, Hyatt AD, Muller R & Speare R (2004) Origin of the amphibian chytrid fungus. *Emerging Infectious Diseases* 10: 2100-2105.
- Werger MJA (1978) Biogeographical division of southern Africa. In: Werger MJA (ed) *Biogeography and ecology of southern Africa*. Dr W. Junk Publishers, The Hague, The Netherlands, *Monographiae biologicae* 31: 145-170.
- White F (1983) The vegetation map of Africa. Unesco, Paris, France. 1-356.
- White TJ, Bruns T, Lee S & Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ & White TJ (eds) *PCR protocols: A guide to methods and applications*. California, Academic Press, San Diego, USA. 315-322.
- Whitfield SM, Kerby J, Gentry LR & Donnelly MA (2012) Temporal variation in infection prevalence by the amphibian chytrid fungus in three species of frogs at La Selva, Costa Rica. *Biotropica* 44: 779-784.
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Wieczorek AM & Channing A (1997) The taxonomic status of Broadley's reed frog. *African Journal of Herpetology* 46: 110-116.
- Wieczorek AM, Channing A & Drewes RC (1998) A review of the taxonomy of the *Hyperolius viridiflavus* complex. *Herpetological Journal* 8: 29-34.
- Wieczorek AM, Drewes RC & Channing A (2000) Biogeography and evolutionary history of *Hyperolius* species: application of molecular phylogeny. *Journal of Biogeography* 27: 1231-1243.
- Wieczorek AM, Drewes RC & Channing A (2001) Phylogenetic relationships within the *Hyperolius viridiflavus* complex (Anura: Hyperoliidae), and comments on taxonomic status. *Amphibia-Reptilia* 22: 155-166.
- Williams PH, de Klerk HM & Crowe TM (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26: 459-474.
- Willis, KJ, Bennett KD, Burrough SL, Macias-Fauria M & Tovar C (2013) Determining the response of African biota to climate change: using the past to model the future. *Proceedings of the Royal Society B* 368: 20120491.
- Wilson KA, Carwardine J & Possingham HP (2009) Setting conservation priorities. *Annales of the New York Academy of Sciences* 1162: 237-264.
- Wilson KA, McBride MF, Bode M & Possingham HP (2006) Prioritizing global conservation efforts. *Nature* 440: 337-340.
- Wintle BA, Walshe TV, Parris KM & McCarthy MA (2012) Designing occupancy surveys and interpreting non-detection when observations are imperfect. *Diversity & Distributions* 18: 417-424.
- Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes J-A, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luoto M, Maiorano L, Nilsson M-C, Normand S, Öckinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P & Svenning J-C (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15-30.



Wollenberg KC, Jenkins RKB, Randrianavelona R, Ralisata M, Rampilamanana R, Ramanandraibe A, Ravoahangimalala OR & Vences M (2010) Raising Awareness of Amphibian Chytridiomycosis will not alienate ecotourists visiting Madagascar. *EcoHealth* 7: 248-251.

Woodhams DC, Alford RA, Briggs CJ, Johnson M & Rollins-Smith LA (2008) Life-history trade-offs influence disease in changing climates: strategies of an amphibian pathogen. *Ecology* 89: 1627-1639.

Woodhams DC, Ardipradja K, Alford RA, Marantelli G, Reinert LK & Rollins-Smith LA (2007) Resistance to chytridiomycosis varies among amphibian species and is correlated with skin peptide defenses. *Animal Conservation* 10: 409-417.

Young BE, Lips KR, Reaser JK, Ibañez R, Salas AW, Cedeño JR, Coloma LA, Ron S, La Marca E, Meyer JR, Muñoz A, Bolaños F, Chaves G & Romo D (2001) Population declines and priorities for amphibian conservation in Latin America. *Conservation Biology* 15: 1213-1223.

Zeisset I & Beebee TJC (2008) Amphibian phylogeography: a model for understanding historical aspects of species distributions. *Heredity* 101: 109-119.

Zimkus BM, Rödel M-O & Hillers A (2010) Complex patterns of continental speciation: molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution* 55: 883-900.



7 Appendices

App. 3.1

App. 3.1.1

Phrynobatrachus tissue (in italic: no voucher, tissue sample only) and voucher specimens examined for genetic and morphological comparison. For further comparative material see Rödel & Ernst (2002b), Hillers et al. (2008, 2009 in press). MOR: field numbers M.-O. Rödel / A. Hillers; GB: GenBank accession numbers

Phrynobatrachus alleni: ZMB 70692, MOR P5, GB: EU718713, female, Côte d'Ivoire, Mont Péko National Park, 06°53.259' N, 07°10.005' W, 21 May 2000, R. Ernst and M.-O. Rödel; ZMB 70693, MOR P4 and ZMB 70694, MOR P6, both males, both same collection details as ZMB 70692.

Phrynobatrachus annulatus: ZMB 70690 (MOR WOL92, GB: EU718714), forest over river, on one side stream with small waterfall, many shrubs, N 08°02.023', W 09°44.143', North Lorma National Forest, Liberia, 22 November 2005, A. Hillers.

Phrynobatrachus batesii: ZMB 70695, MOR K MK, male, Cameroon, Mount Kupe, W. Böhme; MCZ 136783, GB: EU718715, Cameroon, Southwest, E of Ntale Village, Banyang Mbo Forest Reserve, N/NW of Ntale Plateau, 05°15' N, 09°36' E.

Phrynobatrachus calcaratus: MOR FD78 (GB: EU718717), partly dry stream "Boulibhabi" in savannah, with a few trees as gallery, N 11°44.221', W 12°41.099', Fouta Djallon / Forêt de Nialama, Guinea, 2 June 2006, N.-S. Loua & A. Hillers; ZMB 70696 (MOR AM30, GB: EU718716), stream in valley, small gallery forest, near corn, cassava and banana plantations, N 06°50.429', E 00°25.582', Amedzofe, Ghana, 13 July 2005, A.C. Agyei & A. Hillers.

Phrynobatrachus cornutus: ZMB 70745 (MOR DS29, GB: EU718719), Bai Hokou, saline and forest puddles, N 02°51.576', E 16°28.050', Bayanga, Dzanga-Sangha Forest Reserve, Central African Republic, 22 June 2003, M.-O. Rödel.

Phrynobatrachus fraterculus: MOR GO31 (GB: EU718721), old diamond mines and ponds within forest, partly open area, and forest around this area, N 07°27.376', W 10°41.736', Gola National Forest, Liberia, 29 November 2005, A. Hillers.

Phrynobatrachus ghanensis: MOR BTR0503 (GB: EU718722), N 5°31'55.58", W 02°37'07.26", Boi Tano Forest Reserve, Ghana, 30 October 2003, A.C. Agyei & R. Ernst.

Phrynobatrachus guineensis: MOR T13 (GB: EU718723), primary rainforest, Taï National Park, Côte d'Ivoire.

Phrynobatrachus gutturosus: MOR C9 (GB: EU718724), primary rainforest, Taï National Park, Côte d'Ivoire.

Phrynobatrachus liberiensis: Côte d'Ivoire: ZMB 71563 (MOR B03.7), swampy forest, N 05°23.104', W 04°03.072', Banco Natianl Park, 4 September 2003, Rödel, Assemian, Tohé & Kouamé; ZMB 71558, May 2002, other data same as ZMB 71563; ZMB 71557, SRET station, Taï National Park, Côte d'Ivoire, M.-O. Rödel; MOR T4, GB: FJ415753), primary rain forest, Taï National Park, Côte d'Ivoire, 30 May 2000, R. Ernst & M.-O. Rödel; Ghana: ZMB 70725 (MOR ANK68, GB: FJ415754), and ZMB 70726, primary forest with brook and swampy area, with *Raphia* palms, N 05°15.714', W 02°38.703', 8 August 2005, A.C. Agyei & A. Hillers; MOR ANK127, GB: FJ415755, primary forest near stream, partly swampy, N 05°16.642', W 02°38.253', Ankasa Conservation Area, 2 April 2007, C.O. Boateng & A. Hillers; ZMB 70727-29 (MOR KAK77, GB: FJ415756; KAK79, GB: FJ415757; KAK81, GB: FJ415758), forest with swampy area and stream, N 05°26.819', W 01°24.873', Kakum National Park, 10 & 11 August 2005, A.C. Agyei & A. Hillers; MOR KAK50, GB: FJ415759 & KAK80, GB: FJ415760, near stream within primary forest, N 05°21.208', W 01°22.875' & N 05°26.819', W 01°24.873', Kakum National Park, 12 August 2005, A.C. Agyei & A. Hillers; ZMB 71559 (MOR DRR0308), N 5°09' 41.95", W 2°23' 31.16", Ghana Draw River, 23 October 2003, A.C. Agyei & R. Ernst; Guinea: ZMB 71561-71562 (MOR 242; MOR 470), forest, Foma and Banko villages, Pic de Fon / Simandou, 19 August & 3 October 2004, M.A. Bangoura & K. Kamara; ZMB 71554-71555 (MOR FO59-60), secondary and primary forest, app. 6 km from Banko, app. 1.5 km within forest reserve, N 08°31.499', W 08°56.20', 650 m a.s.l., Simandou, 2 December 2002, M.A. Bangoura & M.-O. Rödel; ZMB 71552-71553 (MOR Gu102-103), primary forest, N 07°35'49.7", W 08°12.02.9", Diécké Classified Forest, 21-23 November 2003, M.A. Bangoura & M.-O. Rödel; ZMB 71556 (MOR Gu267), swamp in degraded forest, N 08°08'37.0", W 08°33'17.7", Mont Béro Classified Forest, 5 December 2003, M.A. Bangoura & M.-O. Rödel; ZMB 71551 (MOR Gu33), secondary forest, 444 m, N 07°36'13.2", W 08°12'42.3", Déré Classified Forest, 17 November 2003, M.A. Bangoura & M.-O. Rödel; Liberia: MOR WOL50 GB: FJ415761, primary forest with slightly swampy area and creek, near river, N 08°01.434', W 9°44.414', North Lorma National Forest, 21 November 2005, A. Hillers; MOR GRE6 GB: FJ415762, swampy area in forest with small stream, with many treefall gaps and lianas, N 05°24.358', W 07°44.106', Grebo National Forest, 8 December 2005, A. Hillers; Sierra Leone: ZMB 71560 (MOR LOM105, GB: FJ415763) primary forest around sandy, rocky stream, soil very sandy, only thin leaf litter layer, N 09°13.424', W 11°09.511', 749 m, Loma Mountains, 3 July 2007, J. Johnny & A. Hillers; MOR GOL34, GB: FJ415764, primary forest near stream, with rocks, dry forest as well as lightly swampy area, N 07°34.869', W 11°01.012', Gola North Forest Reserve, 15 September 2005, A. Barrie & A. Hillers; MOR NIM40, GB: FJ415765, swampy area near stream, bamboo, N 08°29.554' W 11°12.385', Nimini North Forest Reserve, 21 September 2005, A. Barrie & A. Hillers; MOR JP0151, GB: FJ415766, swampy area and small



stream in forest with many palm trees and ferns, N 08°29.556', W 11°09.558', 487 m, Nimini Forest Reserve, 9 June 2007, J. Johnny & A. Hillers.

Phrynobatrachus natalensis: ZMB 70730 (MOR Gu110, GB: EU718726), puddles on forest road, N 07°35'46.9", W 08°52'18.8", 454 m, Diécké Classified Forest Guinea, 21-23 November 2003, M.A. Bangoura & M.-O. Rödel.

Phrynobatrachus phyllophilus: MOR GOL35 (GB: EU718727), primary forest near stream, with rocks, dry forest as well as lightly swampy area, N 07°34.869', W 11°01.012', Gola North Forest Reserve, Sierra Leone, 15 September 2005, A. Barrie & A. Hillers.

Phrynobatrachus pinto: ZMB 70689 (MOR BO167, GB: EU718711), gallery forest, N 11°06.377', W 13°57.595', Boké Préfecture/Sangaredi, Kewewol, Guinea, 5 May 2005, A. Hillers, N.S. Loua & M.A. Bangoura.

Phrynobatrachus plicatus: Côte d'Ivoire: ZMB 71547-71549, MOR T11-12, 20, Taï National Park, 30 May 2000, R. Ernst & M.-O. Rödel; Ghana: ZMB 71204 (MOR OWS13), forest, N 06°44.476', W 01°42.400', Owabi Wildlife Sanctuary, 30 July 2005, A.C. Agyei & A. Hillers; ZMB 71206 (MOR KAK23), near stream within forest, N 05°26.916', W 01°25.009', Kakum National Park, 9 August 2005, A.C. Agyei & A. Hillers; MOR KAK17; GB: FJ415767, near stream within forest, N 05°27.000', W 01°24.983', Kakum National Park, 10 August 2005, A.C. Agyei & A. Hillers; ZMB 71202 (MOR ANK132, GB: FJ415768), camp, open area within forest, N 05°16.916', W 02°38.498', Ankasa Conservation Area, 2 April 2007, C.O. Boateng & A. Hillers; ZMB 71207 (MOR ANK63, GB: FJ415769), road within forest, N 05°16.485', W 02°38.790', Ankasa Conservation Area, 7 August, A.C. Agyei & A. Hillers; ZMB 71550 (MOR DRR1903), N 5°09' 41.95", W 02°23' 31.16", Draw River, 26 October 2003, A.C. Agyei & E. Ernst; ZMB 71541 (MOR JP0016), forest, Atiwiredu, N 06°12'22.7", W 00°34'39.2", 817 m, Atewa Range Forest Reserve, 7 June 2006, N.G. Kouamé & C.O. Boateng; ZMB 71205 (MOR TOF15), dry forest, N 06°46.374', W 02°02.538', Tano Offin Forest Reserve, 1 August 2005, A.C. Agyei & A. Hillers; ZMB 71542 (MOR AF9, GB: FJ415770), forest around small stream in valley, N 6°15'16.6" W 2°17'41.7", Afao Hills, 28. March, C.O. Boateng & A. Hillers; ZMB 71543 (MOR ATE9), dry primary forest, N 06°12.367', W 00°34.675', Atewa Forest Reserve, 14 April 2007, C.O. Boateng, A. Hillers & G. Segbiagbeto; MOR BOB2, GB: FJ415771, puddles and borders along road within forest, N 06°41.422', W 01°19.485', Bobiri Forest Reserve, 25 July 2005, A.C. Agyei & A. Hillers; Guinea: ZMB 71544-71545 (MOR Gu117-118), primary forest, N 07°35'49.7", W 08°12.02.9", Diécké Classified Forest, 21-23 November 2003, M.A. Bangoura & M.-O. Rödel; ZMB 71546 (MOR Gu231), river and gallery forest, N 08°08'20.7", W 08°34'23.7", Mont Béro Classified Forest, 2 December 2003, M.A. Bangoura & M.-O. Rödel; Liberia: ZMB 70738 (MOR GO42), hilly primary forest with stream, stream with rocks and sand, N 07°27.178', W 10°41.522', Gola National Forest, 30 November 2005, A. Hillers; ZMB 70739 (MOR WOL71), forest over river, on one side stream with small waterfall, many shrubs, N 08°02.023', W 09°44.143', North Lorma National Forest, 22 November 2005, A. Hillers; MOR GRE19, GB: EU718728, N 05°24.285', W 07°43.786', swampy area within secondary forest near stream with many lianas and shrubs, thick leaf litter coverage, Grebo National Forest, 9 December 2005, A. Hillers; ZMB 70737 (MOR GRE30), forest next to swampy area, Grebo National Forest, 05°24.358' N, 07°44.106' W, 10 December 2005, A. Hillers; Togo: ZMB 71203 (MOR TOG9), narrow gallery forest, almost no trees left and plantations instead, N 08°09.732', E 00°38.718', Yégué, 6 April 2007, A. Hillers.

Phrynobatrachus tokba: MOR GRE77 (GB: EU718729), next to old logging road in secondary forest, N 05°23.827', W 07°44.160', Grebo National Forest, Liberia, 11 December 2005, A. Hillers.

Phrynobatrachus villiersi: ZMB 70743 (MOR T18, GB: EU718730), primary rain forest, Taï National Park, Côte d'Ivoire, 30 May 2000, R. Ernst & M.-O. Rödel.

App. 3.1.2

App. 3.1.2-1

Translations of the original descriptions of *Hyperolius nitidulus* by Peters (1875) and *Hyperolius spatzi* by Ahl (1931a):

Hyperolius nitidulus (Fig. 2): "Body shape equals that of *H. marmoratus*. Snout same length as eye. Tympanum hidden. Belly and ventral surfaces of thighs granular. The outer two fingers and the forth toe, with the exception of the two most distal phalanges, webbed. Dorsally purple grey, shanks likewise colored, whereas the thighs seem to be uncolored. A black band from nose through eye to belly, there band dissolving into black spots on white background; upper lip, flanks below this band, anal region, upper surfaces of forearms, outer and inner edge of shanks and external side of foot to toe tips (in ethanol) white with black spots, which plus/minus fuse. Total length 28 mm; head: 8 mm; head width: 8.5 mm; forearm: 19 mm; hand with 3rd finger: 7 mm; hind leg: 44 mm; foot with fifth toe: 20 mm. From Yoruba (Lagos). [comment added: referring to ZMB 7729, holotype]" Plate 3 (figures 4 and 4a) in Peters (1875) figures the typical wet season color pattern of this species.

Hyperolius spatzi (Fig. 1): "stocky body shape; vomerine teeth absent; choanae very small, hidden below edge of mandible; tongue unusually small, notched posteriorly; large head, app. 1/3 of body length, wider than long; snout rounded, truncated in lateral view, not or only slightly surpassing mouth, as long as eye, much shorter than distance between anterior corner of eyes, slightly longer than high; canthus rostralis rounded but distinct; loreal region vertical, only slightly concave; narines in mid distance between eye and snout-tip; inter-narial distance slightly narrower than inter-orbital distance, the latter twice as wide as upper eyelid; tympanum hidden beneath skin.



Robust fingers, 1/3 to 1/2 webbed; well developed discs; 1st finger shorter than second, second shorter than fourth, which is slightly surpassed by the 3rd finger; 3rd finger as long as snout; subarticular tubercles moderately large, not prominent. Webbing on feet complete with the exception of 4th toe where the last phalanx is without webbing; discs as large as those on fingers; 5th toe slightly longer than 3rd; external metatarsalia tightly fused, tarsal fold absent; very small inner metatarsal tubercle; outer metatarsal tubercle lacking; no tarsal tubercle; subarticular tubercle small, moderately distinct. Tibio-tarsal angle surpasses eye or reaches snout-tip. Femur shorter than tibia, the latter 3.5–4 times longer than wide and twice or slightly less times in body length, longer than foot; heels in contact when hind legs arranged to body at right angles.

Dorsal skin thick, almost leathery, rough, beset with many small smooth or rough warts; ventrum granular; distinct postgular and postpectoral folds; no temporotemporal fold; males with subgular vocal sac and a small, indistinct gular flap.

Coloration in alcohol dorsally chalk white or, rarer, fine speckled with dark-brown. Venter white. Ventral parts of thighs and inner parts of shanks flesh-colored (presumably red in life). No markings at all.

Body length 21 mm. Bakel-Kidira (Upper Senegal region). 26 specimens, Bakel-Kidira, Spatz leg., types [comment added: ZMB 32602, lectotype; 74853-74876, paralectotypes; formerly all ZMB 32602]. The species is named to honor the collector, the well know researcher Spatz, whose collecting activities resulted in a large number of valuable reptiles and amphibians, stored in the Berlin museum."

App. 3.1.2-2

Voucher specimens, including types, of *Hyperolius spatzi* and *H. nitidulus* in the ZMB and SMNS collections.

Hyperolius nitidulus. Benin: ZMB 74896-74898, Pendjari National Park, Sudan savanna, October 2003, coll. Olaf Grell; ZMB 74890, Pendjari National Park, Tangieta, savanna, N 10°38.317', E 01°15.746', 1 September 2004, coll. G.A. Nago & M.-O. Rödel; Burkina Faso: ZMB 74893-74894, Dano, small river in savanna, N 11°14'16.8", W03°01'24.1", 22 October 2003, coll. T. Moritz; Ivory Coast: SMNS 8995.1-2, Ananda, 1993, coll. M.-O. Rödel; SMNS 9680.1-2, Bondoukou, 1996, coll. K. Kouadio; ZMB 74888 & SMNS 8967.1-7, Comoé National Park, savanna, June 1996, coll. M.-O. Rödel; ZMB 74886, Mont Sangbé National Park, Mare Soumarou, island forest in the savanna, pitfall trap, dry season 2001, coll. G. Gbmalin & Y. Cesar; Guinea: ZMB 74895, Mont Béro Classified Forest, savanna, N 08°08'30.9", W08°34'09.6", 1 December 2003, coll. M.A. Bangoura & M.-O. Rödel; ZMB 74891-74892 Nimba Mountains, savanna Séringbara, with big ponds, close to village, N 07°36.181', W08°29.769', 18 May 2006, coll. T.N.-S. Loua & A. Hillers; ZMB 74889, Pic de Fon/Simandou range, Banko, savanna, 11 July 2004, coll. M.A. Bangoura & K. Kamara; ZMB 74882, Boké Préfecture/Kolaboui, swampy area in secondary forest island, N 10°45.075', W14°27.040', 23 & 24 April 2005, coll. M.A. Bangoura & A. Hillers (originally listed as *H. spatzi* in Hillers et al. 2006); Nigeria: ZMB 7729 (holotype), Yoruba (Lagos), coll. Krause; Sierra Leone: ZMB 74884-74885, Tingi Hills, big pond with a few trees around and swampy area in savanna, N 08°51.047', W10°46.502', 427 m a.s.l., 5 June 2007, coll. J. Johnny & A. Hillers; Togo: ZMB 39028, station Sokode, coll. Schröder.

Hyperolius spatzi. Gambia: ZMB 74877, Abuko Nature Reserve, savanna, 2005, coll. L. Barnett & C. Emms; Senegal: ZMB 32602 (lectotype), 74853-74876 (paralectotypes, formerly all ZMB 32602), Bakel-Kidira, coll. Spatz; ZMB 74279, Sabodala, ponds and puddles in degraded farmbrush savanna next to Oromin camp, N 13°09.368', W 12°06.882', 12 September 2009, coll. A. Hillers & Y. Mané; ZMB 74280-74285, Sabodala, in and around big pond in farmbrush savanna/grassland, with some rocks, N 13°07.259', W 12°07.622', 7 September 2009, coll. A. Hillers & Y. Mané.

App. 3.1.3

Astylosternus occidentalis vouchers examined. Provided are collection accession numbers, in parenthesis: age/sex and size; geographic data are presented as latitude/longitude; data presented in italics refer to specimen where only tissue samples are available at the ZMB.

Ivory Coast: ZMB 75349 (male, 61 mm), Haute Dodo Forest Reserve, 4.9 / -7.4, small brook in degraded rainforest; PEM A7921 (female, 62 mm); same data as ZMB 75349; MNHN 1993.6074 (female, 54.2 mm), 1993.6075 (female, 58.1 mm), 1993.6076 (female, 54.2 mm), 1995.6077 (female, 54.1 mm), 1993.6078 (male, 50.3 mm), 1993.6079 (female, 60.0 mm), Mont Tonkoui; ZMB 75353-75354 (male, 49.9 mm; female, 54.8 mm), Mont Sangbé National Park, fast flowing forest stream; ZMB 75353 (male, 49.8 mm), other data as ZMB 75354; ZMB 75346 (male, 53.8 mm), village Ponan, close to Taï National Park; ZMB 75347-75348 (male, 56.7 mm; female, 63.8 mm), Taï National Park, 1st bridge to IET station, swampy secondary forest and shallow creek; ZMB 75350 (subadult, 44.2 mm), Taï National Park, primary rainforest near Inselberg 90; SMNS 9611 (male, 58.1 mm), Taï National Park, South Camp, primary rainforest; SMNS 9612 (subadult, 44.7 mm), Taï National Park, Töp Grid, on path in primary rainforest; SMNS 9613.1 (metamorph, 28.8 mm), SMNS 9613.2 (tadpole), Taï National Park, Mont Nienokoué, fast flowing creek; SMNS 9614 (female, 47.5 mm), Taï National Park, transect III, part 12, on dirt road in rainforest; ZMUC R 075609 (subadult, 43.7 mm), Zeala.

Guinea: ZMB 75364 (male, 46.2 mm), Pic de Fon, Simandou Range, Wisky 1, mountain forest; ZMB 75365 (male, 51.2 mm), Pic de Fon, Simandou Range, Kabakanga; ZMB 75366 (male, 44.5 mm), Pic de Fon, Simandou Range, 8.5 / -8.9, Foma, mountain forest; ZMB 75367 (male, 51.1 mm), Pic de Fon, Simandou Range, Oueleba, source in



mountain forest; ZMB 75357 (female, 57.2 mm), Pic de Fon, Simandou Range, Oueleba forest, N'KoKong, Tiyeo near Traorela, village NE of Pic de Fon, gallery forest at mountain base; ZMB 75371 (subadult, 48.3 mm), Simandou Range, 8.6 / -8.9, altitude savanna, on dirt road; ZMB 75369 (male, 48.1 mm), SI18 (male, 49.4 mm), Simandou Range, Damaro, 9.2 / -8.9, gallery forest, in altitudinal savanna, with river, water falls and many caves; MNHN 1999.7349 (subadult, 43.4 mm), Simandou Range, Sénélogou Hill, 750 m a.s.l.; ZMB 75461 (male, 61.4 mm), Mount Béro, 8.3 / -8.7, 905 m a.s.l.; MTN4 (female, 61.8 mm), ZMB 75362 (female, 61.2 mm), Nimba mountains, 7.7 / -8.4, gallery forest, river Zié, Zié valley; MTN84 (male, 49.6 mm), ZMB 75363 (MTN87, male, 47.8 mm), Nimba mountains, 7.7 / -8.4, small gallery forest in Gégué valley; MTN243 (male, 53.7 mm), Nimba mountains, 7.7 / -8.4, small gallery forest in savanna "de buttes" along river Yè; MTN34 (juvenile, 34.6 mm), MTN37 (juvenile, 34.1 mm), Nimba mountains, 7.7 / -9.5, savanna of Séringbara/Cavally, pond and small gallery forest; MTN92 (male, 47.2 mm), Nimba mountains, 7.7 / -8.4, forest close to Nimba camp; ZMB 37564 (2 tadpoles), Nimba mountains; MNHN 1994.5574-1994.5579 (tadpoles), 1970.695 (subadult, 44.5 mm), Nimba mountains; MNHN 1993.4072-1993.4081 (tadpoles), Nimba mountains, stream Mieu near Bié; MNHN 1970.696 (female, 54.1 mm), Nimba mountains, Bié dirt road, forest; MNHN 1970.697 (female, 58.6 mm), Nimba mountains, Yalé, 20 October 1956; MNHN 1970.692 (female, 55.0 mm), 1970.693 (female, 55.9 mm), 1970.694 (female, 55.0 mm), Nimba mountains, Ziéla; MNHN 1999.7338 (female, 51.1 mm), Nimba mountains, edge Zougné; MNHN 1999.7343 (subadult, 44.0 mm), Nimba mountains, Gouela; MNHN 1999.7340 (metamorph with rest of tail, 35.5 mm), Nimba mountains region, Nion forest; ZMB 75377 (male, 56.1 mm), Famoula, 8.9 / -8.6, gallery forest with rocky river; ZMB 75376 (male, 48 mm), Mont Tibé, 8.8 / -8.9, river with small gallery forest surrounded by savanna; ZMB 77317 (2 tadpoles), Déré forest, 419 m a.s.l.; ZMB 75370 (male, 50.0 mm), Sinko, 8.9 / -8.3, gallery forest; ZFMK 56289 (female, 57.9 mm), Prefecture Macenta, Sérédou; ZFMK 58651 (subadult, 43.3 mm), Ziama Forest Reserve, Malweta; ZMB 75464-75465 (female, 59.5 mm; male, 61.8 mm), Ziama Forest Reserve, 8.4 / -9.3, 562 m a.s.l.; ZMB 77440 (tadpole), Ziama Forest Reserve, 664 m a.s.l.; ZMB 75360 (metamorph, 27.5 mm), Boké Préfecture, Sangaredi Bentou, 11.1 / -14.0, river with gallery forest; FD17 (juvenile, 30.7 mm), ZMB 75351 (metamorph, 28.4 mm), ZMB 77438 (tadpole), Fouta Djallon, Chutes de Sala, 11.3 / -12.5, forest, partly swampy area, small stream; FD20 (juvenile, 31.4 mm), Fouta Djallon, Chutes de Sala, 11.3 / -12.5, forest, next to river, partly degraded; ZMB 75466 (male, 49.5 mm), Fouta Djallon, Labé/Saala, 11.3 / -12.5, 897 m a.s.l.; ZMB 75462 (subadult, 40.5 mm), Fouta Djallon, Labé/Saala, 11.3 / -12.5, 865 m a.s.l.; ZMB 75467-75469 (female, 54.0 mm; male, 52.5 mm; male, 47.8 mm), ZMB 77439 (2 tadpoles), Fouta Djallon, Dalabé/Chute de Detin, 10.8 / -12.2, 760 m a.s.l.; ZMB 75463 (male, 53.9 mm), Fouta Djallon, Dabola/Kolon, 10.9 / -10.9, 830 m a.s.l.; ZMB 75492 (female, 55.4 mm), Boffa Region, 10.7 / -13.8, forest-savanna mosaic, 132 m a.s.l.; ZMB 75488-75491 (male, 49.5 mm; male, 49.5 mm; male, 50.0 mm; male, 50.4 mm), Boffa Region, 10.8 / -13.8, degraded gallery forest, waterfalls and rapids, 359 m a.s.l.; ZMB 75493-75494 (male, 49.1 mm; male, 52.2 mm), Boffa Region, 10.8 / -13.7 degraded forest in valley, creek with little flow rate, 229 m a.s.l.; ZMB 75495 (female, 50.1 mm), Boffa Region, 11.0 / -13.7, heavily degraded gallery forest, 316 m a.s.l.; ZMB 77226 (juvenile, 33.6 mm), ZMB 77227 (female, 58.2 mm), ZMB 77228 (female, 59.8 mm), ZMB 77229 (female, 49.2 mm), ZMB 77230 (male, 51.2 mm), ZMB 77231 (female, 60.0 mm), ZMB 77232 (juvenile, 43.5 mm), Prefecture Macenta, region, N'Zérékoré, 8.0 / -9.1, 460 m a.s.l., degraded tree-savanna/frambush; ZMB 77233 (female, 62.1 mm), Prefecture Yomou, region N'Zérékoré, 8.0 / -9.1, 540 m a.s.l., degraded tree-savanna/frambush; ZMB 77234 (female, 53.7 mm), Prefecture Yomou, region N'Zérékoré, 8.0 / -9.1, 780 m a.s.l., degraded tree-savanna/frambush; ZMB 77235 (female, 57.0 mm), ZMB 77236 (juvenile, 46.5 mm), Prefecture Yomou, region N'Zérékoré 7.6 / -9.2, 420 m a.s.l., degraded tree-savanna/frambush; ZMB 77239 (female, 50.9 mm), ZMB 77240 (male, 54.4 mm), ZMB 77241 (female, 53.4 mm), ZMB 77242 (male, 56.0 mm), ZMB 77243 (female, 55.0 mm), ZMB 77244 (female, 62.8 mm), ZMB 77245 (male, 57.9 mm), ZMB 77246 (female, 53.2 mm), Prefecture Kerouané, region Kankan, 9.0-9.2 / -8.9 - -9.0, 760-1330 m a.s.l., degraded shrub and tree-savanna/farmbrush.

Liberia: MNHN 1951.233a (female, 53.8 mm), 1951.231 (female, 60.6 mm), 1951.232 (subadult, 46.7 mm), 1951.233 (subadult, 45.9 mm), 1951.234 (female, 49.9 mm), 1951.235 (female, 55.8 mm), 1951.236 (subadult, 47.0 mm), 1952.123 (male, 57.5 mm), 1952.124 (female, 56.5 mm), 1995.3188 (subadult, 48.8 mm), Nimba mountains; MNHN 1999.7351 (female, 52.2 mm), 1999.7352, 1999.7353 (female, 54.4 mm), Nimba mountains, Grassfield; MNHN 1999.7341 (male, 53.2 mm), Nimba county, Mont Bele; MNHN 1999.7342 (subadult, 45.4 mm), Mount Tokadeh; ZMB 75355 (female, 56.2 mm), Mount Tokadeh, River Poa, 7.5 / -8.7, 537 m a.s.l.; ZMB 75352 (female, 52.5 mm), GO58 (male, 64.6 mm), Gola National Forest, 7.5 / -10.7, hilly primary forest with stream, stream with rocks and sand; GO29 (male, 53.3 mm), Gola National Forest, 7.5 / -10.7, valley within forest with small brook, partly swampy area and forest around, partly on hill; ZMB 75470-75471 (female, 52.5 mm; female, 58.0 mm), Putu Range, 5.7 / -8.2, Slabbert's Ville, 306 m a.s.l.; ZMB 75472 (subadult, 42.2 mm), Putu Range, 5.7 / -8.2, Camp2, 283 m a.s.l.; ZMB 75473 (female, 59.3 mm), ZMB 75479 (female, 54.7 mm), Putu Range, 5.7 / -8.2, T14, 257 a.s.l.; ZMB 75474 (female, 56.0 mm), Putu Range, 5.7 / -8.1, T16, 264 m a.s.l.; ZMB 75475 (female, 56.7 mm), Putu Range, 5.7 / -8.1, pitfall4, 195 m a.s.l.; ZMB 75476-75477 (female, 56.2 mm; LI206, female, 52.2 mm), Putu Range, 5.7 / -8.1, T20, 204 m a.s.l.; ZMB 75478 (female, 60.1 mm), Putu Range, 5.6 / -8.2, T25, 243 m a.s.l.; ZMB 75838 (male, 51.4 mm), Wakolor Forest, 6.7 / -11.4, swamp in farmbrush area; ZMB 77237 (male, 59.9 mm), ZMB 77238 (male, 53.9 mm), Zota District, Bong County, 7.2 / -9.3, 400 m a.s.l., farmbrush.

Sierra Leone: BMNH 1947.2.5.48 (holotype, male, 59.3 mm), Sandaru, East Sierra Leone; ZMB 75372 (male, 46.7 mm), Gola Forest, Seliti, 7.4 / -11.3, stream at edge of secondary forest, swampy area around stream; ZMB 75373 (female, 55.3 mm), Gola Forest, Gola North, 7.7 / -10.9, forest and big stream; ZMB 75368 (3 tadpoles), Gola North, 7.7 / -10.8, very small forest brook, clear and running; GS175 (female, 56.3 mm, specimen at Gola Forest Project), Gola Forest, Extension 2, 7.8 / -10.6, hilly secondary forest around stream; ZMB 75374 (male, 53.2 mm), Loma mountains, 9.2 / -11.1, 1480 m a.s.l., gallery forest and montane grassland next to this forest; ZMB 75375 (female, 62.2 mm), Loma mountains, 9.2 / -11.2, 749 m a.s.l., primary forest around sandy, rocky stream, soil very sandy, only thin leaf litter layer; ZMB 75359 (female, 56.2 mm), Loma Mountains Forest Reserve, 9.2 / -11.1, primary forest with



stream; LOM12 (55.6 mm), Loma Mountains Forest Reserve, 9.2 / -11.1, primary forest with stream; ZMB 75358 (female, 55.0 mm), Nimini North Forest Reserve, 8.5 / -11.2, near stream near road and village Peya; ZMB 75378 (female, 57.3 mm), Nimini Forest Reserve, 8.5 / -11.1, 509 m a.s.l., river Bakuya, partly in forest, partly with narrow gallery forest, next to open area with houses ("village" Bakuya) and plantation; NIM103 (male, 45.4 mm), Nimini Forest Reserve, 8.5 / -11.1, forest next to stream, mainly pristine, partly many lianas; NIM119 (juvenile, 35.7 mm), Nimini Forest Reserve, 8.5 / -11.1, 322 m a.s.l., degraded and hilly forest with rocky streams, forest dry on slopes, otherwise more humid areas with palm trees and Marantaceae; ZMB 75361 (female, 57.9 mm), Western Area Peninsula Forest Reserve, 8.3 / -13.2, forest with rocky river; ZMB 75356 (juvenile, 34.1 mm), Tingi Hills, 8.9 / -10.8, 725 m a.s.l., forest next to large, rocky river; TI28 (juvenile, 33.2 mm), Tingi Hills, 8.9 / -10.8, 718 m a.s.l., primary forest next to large stream; ZMUC R 074932 (male, 49.8 mm), R 075996 (male, 49.2 mm), Kassewe, stream in forest.

App. 3.2

App.3.2-1

Table of amphibian assemblages used in the study. The first column lists the countries and the second the name of the site. Abbreviations are as follows in order of appearance: columns 3 to 6: no. of families per site - Fam.; no. of genera per site - Gen.; no. of total species listed per site - Spec.; no. of species listed as undescribed - Und.; columns 7 to 13 (IUCN red list categories): not listed - NL; data deficient - DD; least concern - LC; near threatened - NT; vulnerable - VU; endangered - EN; critically endangered - CR; columns 14 to 19: no. of species occurring outside West Africa - RA; no. of local endemics occurring outside West Africa - RLE; no. of species occurring only west of the Cross River - WC; no. of species occurring only west of the Dahomey gap - WD; no. of species occurring only in Upper Guinea - UG; no. of West African local endemics - WLE. Taxonomy for all species has been harmonised according to Frost (2010) and publications not yet included in this database (Blackburn *et al.* 2009; Rödel *et al.* 2009a, b, c, d; Barej *et al.* 2010), updated and corrected where necessary.

Country	Site	Fam.	Gen.	Spec.	Und.	NL	DD	LC	NT	VU	EN	CR	RA	RLE	WC	WD	UG	WLE	Source
Bénin	Bohicon/Lama	10	11	26	0	3	0	23	0	0	0	0	22	0	4	0	0	0	Rödel <i>et al.</i> 2007; Ullenbruch unpubl.
Bénin	Pendjari	11	15	31	0	1	0	30	0	0	0	0	24	0	6	1	0	0	Nago <i>et al.</i> 2006
Cameroon	Korup	12	32	83	8	10	3	55	4	4	7	0	70	10	3	0	0	0	Lawson 1993
Cameroon	Kupe	5	15	37	2	2	1	22	3	4	5	0	35	2	0	0	0	0	Schmitz <i>et al.</i> 1999; Schmitz unpubl.
Cameroon	Manengouba	9	20	62	9	10	2	26	3	7	13	1	48	11	2	0	1	0	Gonwouo & Rödel unpubl.
Cameroon	Nkongsamba	9	24	75	3	5	0	44	5	7	12	2	68	5	2	0	0	0	Amiet 1975



Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Congo (Rep.)	Congo (Rep.)	Congo (Rep.)	Central African Republic	Cameroon	Cameroon
Lamto	Haute Dodo	Comoé	Cavally	Bossématié	Banco		Lac Tété	Nouabale-Ndoki	Kouilou	Dzanga	Tchabal	Mt Nlonako
11	11	10	10	4	9		9	8	10	12	7	10
13	16	14	15	5	13		12	10	17	19	10	28
39	36	32	33	8	27		17	19	34	46	16	86
0	1	0	0	0	1		2	0	0	5	7	3
3	6	1	3	0	4		2	0	0	6	7	4
1	0	0	0	0	0		0	1	0	1	1	0
32	18	31	17	7	18		15	18	34	39	3	57
3	8	0	8	1	3		0	0	0	0	0	7
0	2	0	4	0	1		0	0	0	0	4	6
0	2	0	1	0	1		0	0	0	0	0	12
0	0	0	0	0	0		0	0	0	0	1	0
22	12	23	12	3	13		15	18	33	40	7	79
0	0	0	0	0	0		2	1	0	5	9	3
9	6	7	7	4	3		0	0	1	1	0	3
3	2	1	1	0	0		0	0	0	0	0	0
5	16	1	13	1	10		0	0	0	0	0	1
0	0	0	0	0	1		0	0	0	0	0	0
Lamotte 1967; Adeba et al. 2010	Rödel & Branch 2002; Rödel & Branch 2005	Rödel 2000; Rödel & Spieler 2000	Rödel & Branch 2002; Rödel & Branch 2005	Rödel unpubl.	Assenian et al. 2006 ; Rödel unpubl.	Jackson et al. 2007	Jackson & Blackburn 2007	Largen & Dowsett-Lemaire 1991	Rödel unpubl.	Herrmann et al. 2007	Plath et al. 2004; Herrmann et al. 2005	



Gabon	Gabon	Gabon	Gabon	Gabon	Equatorial Guinea	Congo (Dem. Rep.)	Congo (Dem. Rep.)	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire	Côte d'Ivoire
Gamba	Mt Doudou	Crystal Mts.	Massif du Chaillu	Forêt des Abeilles	Alen	Virunga	Garamba	Tai	Sangbé	Péko	Marahoué	
9	15	13	8	9	10	10	10	12	12	10	12	
10	28	20	13	16	25	15	14	18	15	14	13	
18	69	43	25	31	50	54	39	53	43	30	31	
2	15	4	0	1	2	0	0	0	1	1	0	
2	18	7	1	1	3	1	1	6	5	3	3	
1	1	1	0	0	0	3	1	2	0	0	0	
15	50	32	23	30	44	42	37	26	32	21	28	
0	0	0	0	0	0	2	0	11	5	5	0	
0	0	0	0	0	1	5	0	3	1	1	0	
0	0	3	0	0	2	1	0	4	0	0	0	
0	0	0	1	0	0	0	0	1	0	0	0	
16	51	35	22	28	45	50	38	18	22	14	22	
2	15	7	1	1	2	2	0	0	0	0	0	
0	3	1	2	2	3	2	0	7	10	7	8	
0	0	0	0	0	0	0	1	2	0	1	0	
0	0	0	0	0	0	0	0	22	10	8	1	
0	0	0	0	0	0	0	0	4	1	0	0	
Burger et al. 2006	Burger et al. 2004; Burger et al. 2006; Pauwels & Rödel 2007	Pauwels & Rödel 2007; Rödel unpubl.	Pauwels & Rödel 2007; Rödel unpubl.	Fretey & Dewynter 1998	De la Riva 1994; Lasso et al. 2002	cited in Vonesh 2001	cited in Vonesh 2001	Ernst & Rödel 2005	Rödel 2003	Rödel & Ernst 2003	Rödel & Ernst 2003	



Ghana	Ghana	Ghana	Ghana	Ghana	Ghana	Ghana	Ghana	Ghana	The Gambia	Gabon	Gabon	Gabon
Bia	Atewa	Apesokubi	Ankasa	Amedzofe, Blakpa & Wli	Ajenjua Bepo	Accra	Kiang West	Abuko	Rabi-Toucan	Loango	Ivindi	
13	12	7	38	24	6	10	7	8	11	10	10	
9	15	8	15	11	6	12	9	11	23	15	18	
7	30	15	10	10	10	18	14	19	46	28	34	
0	0	0	1	1	1	0	0	0	3	2	0	
3	3	2	4	3	4	1	0	1	4	2	0	
0	0	0	0	0	0	0	0	0	0	1	0	
6	18	13	21	18	5	16	14	18	42	25	34	
2	3	0	6	0	1	1	0	0	0	0	0	
1	2	0	3	0	0	0	0	0	0	0	0	
1	3	0	4	2	0	0	0	0	0	0	0	
0	1	0	0	1	0	0	0	0	0	0	0	
5	11	11	16	16	5	16	11	13	41	25	33	
0	0	0	0	0	0	0	0	0	2	2	0	
4	8	4	6	4	1	1	3	5	3	1	1	
0	3	0	1	2	1	0	0	1	0	0	0	
4	8	0	15	2	2	1	0	0	0	0	0	
0	0	0	0	0	1	0	0	0	0	0	0	
Hillers et al. 2009	Kouamé et al. 2007	Rödel & Agyei 2003	Rödel et al. 2005; Hillers et al. 2009	Rödel & Agyei 2003; Hillers et al. 2009	Leaché & Boateng 2009	Leaché 2005; Rödel & Agyei unpubl.	Wanger 2005; Emms et al. 2006	Emms et al. 2006; Barnett et al. 2001	Burger et al. 2006	Burger et al. 2006	Pauwels & Rödel 2007	

134



Guinea	Guinea	Guinea	Guinea	Guinea	Guinea	Guinea	Guinea	Guinea	Guinea/Liberia/ Côte d'Ivoire	Guinea	Guinea	Guinea
Saala	Pic de Fon	Nialama	Kolaboui	Kamsar	Haute Niger	Diéké	Déré	Béro	Nimba	Walewale	Guinea	Ghana
6	12	6	7	6	8	12	8	7	12	6	21	Tano Offin, Subim & Ayum
8	16	7	7	6	9	16	9	10	19	8	10	
14	54	17	13	12	16	46	25	26	59	12	9	
2	3	1	0	0	0	1	0	1	1	0	1	
4	11	2	2	1	1	6	4	6	8	0	2	
0	3	0	0	0	1	1	0	1	4	0	0	
9	29	14	11	10	14	29	14	14	31	12	16	
1	8	1	0	0	0	8	7	4	10	0	3	
0	1	0	0	1	0	1	0	1	1	0	0	
0	2	0	0	0	0	1	0	0	3	0	0	
0	0	0	0	0	0	0	0	0	2	0	0	
5	18	10	7	8	12	19	11	8	20	10	13	
0	0	0	0	0	0	0	0	0	0	0	0	
3	8	4	3	1	3	7	3	4	7	2	5	
0	5	0	2	3	1	2	0	2	4	0	0	
4	21	3	1	0	0	17	11	12	24	0	3	
2	2	0	0	0	0	1	0	0	4	0	0	
Hillers et al. 2008	Rödel & Bangoura 2004a; b	Hillier et al. 2008	Hillers et al. 2006	Hillers et al. 2006	Greenbaum & Carr 2005	Rödel et al. 2004; Rödel & Bangoura 2006	Rödel et al. 2004; Rödel & Bangoura 2006	Rödel et al. 2004; Rödel & Bangoura 2006	Rödel et al. unpubl.	Rödel & Agyei unpubl.	Leaché 2006; Hillers et al. 2009	



Liberia	Liberia	Kenya	Kenya	Kenya	Kenya	Kenya	Kenya	Kenya	Kenya	Guinea	Guinea	Guinea
Grebo	Gola	Tana River Primate	Runda-Gigiri	Meru	Kenya (Limuru)	Kakamega Forest	Mt Elgon	Arabuko- Sokoke	Ziana	Touri	Sangaredi	
9	9	8	6	7	7	9	7	9	10	6	6	
11	12	9	7	7	9	11	8	12	13	8	6	
29	27	16	9	11	18	23	9	24	29	14	14	
2	2	0	0	0	1	0	0	1	0	2	1	
4	5	0	2	1	1	0	0	2	4	2	1	
0	0	0	0	0	0	0	1	1	1	0	1	
16	16	16	7	10	15	23	7	21	19	12	11	
7	4	0	0	0	1	0	0	0	4	0	0	
2	1	0	0	0	1	0	0	0	0	0	1	
0	1	0	0	0	0	0	0	0	1	0	0	
0	0	0	0	0	0	0	1	0	0	0	0	
12	12	16	8	11	17	23	8	23	13	9	6	
0	0	0	1	0	1	0	1	1	0	0	0	
6	5	0	0	0	0	0	0	0	3	1	2	
1	0	0	0	0	0	0	0	0	1	0	3	
10	10	0	0	0	0	0	0	0	11	3	2	
0	0	0	0	0	0	0	0	0	1	1	1	
Hillers & Rödel 2007a; b	Hillers & Rödel 2007a; b	Malonza et al. 2006	Veith 2004	Wasonga & Löters et al. 2007	Veith 2004	Löters et al. 2007	Veith 2004	Poynton 2000; Rödel unpubl.	Rödel et al. 2004	Hillers et al. 2008	Hillers et al. 2006	



Sierra Leone	Senegal	South Africa	South Africa	Nigeria	Nigeria	Nigeria	Nigeria	Nigeria	Nigeria	Nigeria	Mozambique	Liberia
Freetown	Nikola-Koba	Western Cape Province	Kruger	Oyo	Osomba	Ogudu & Iperin	Obudu	Lagos	Ibadan	Niassa	North Lorma	
6	9	6	11	10	8	11	7	9	9	12	6	
8	11	19	20	14	16	15	13	12	12	17	6	
11	24	44	31	28	28	36	24	21	23	28	17	
0	0	0	0	0	0	1	2	1	0	0	2	
1	2	0	1	3	0	7	3	4	3	1	4	
0	0	3	1	0	0	0	0	0	0	0	0	
8	22	29	29	25	25	27	8	17	20	27	9	
1	0	3	0	0	3	2	1	0	0	0	2	
0	0	4	0	0	0	0	8	0	0	0	1	
1	0	3	0	0	0	0	3	0	0	0	1	
0	0	2	0	0	0	0	1	0	0	0	0	
3	16	39	31	25	25	24	20	16	19	28	8	
0	0	5	0	0	0	0	3	0	0	0	0	
0	5	0	0	3	3	8	1	2	4	0	3	
3	3	0	0	0	0	0	0	0	0	0	1	
4	0	0	0	0	0	1	0	1	0	0	5	
1	0	0	0	0	0	3	0	2	0	0	0	
Schiotz 1967	Joger & Lambert 2002	Baard & De Villiers 2000	Pienaar et al. 1963	Schiotz 1967; Onadeko & Rödel 2008	Schiotz 1967	Schiotz 1967; Onadeko & Rödel 2008	Schiotz 1967; Lea et al. 2005	Onadeko & Rödel 2008	Schiotz 1967	Branch & Rödel unpubl.	Hillers & Rödel 2007a; b	



Tanzania	Tanzania	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone	Sierra Leone
Mahenge	Arusha	WAP	Tonkoli	Tiwai	Tama	Nimni	Loma Mts	Kenema	Kassewe	Kamakwie	Gola	
14	7	7	5	8	5	8	11	6	7	4	9	
21	9	8	6	10	6	10	15	9	8	5	13	
40	11	9	11	18	11	19	37	15	18	10	28	
4	0	0	0	0	0	1	1	1	0	0	1	
5	1	1	1	2	2	2	6	3	0	1	4	
1	0	0	0	1	0	1	2	0	0	0	0	
31	9	6	8	10	8	13	23	7	16	8	16	
0	0	1	2	3	1	2	5	5	2	1	7	
1	1	0	0	1	0	1	1	0	0	0	1	
2	0	1	0	1	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	
35	10	4	5	7	6	7	13	4	11	3	9	
5	1	0	0	0	0	0	0	0	0	0	0	
0	0	0	1	1	1	3	6	0	2	0	4	
0	0	0	0	2	0	1	4	0	1	3	2	
0	0	4	5	7	4	7	14	11	4	4	13	
0	0	1	0	1	0	1	0	0	0	0	0	
Loader et al. 2004; Burgess et al. 2007	Razetti & Msuya 2002	Hillers et al. unpubl.	Hillers et al. unpubl.	Hillers et al. unpubl.	Hillers et al. unpubl.	Hillers et al. unpubl.	Lamotte 1971 ; Hillers et al. unpubl.	Schiotz 1967	Schiotz 1967	Schiotz 1967	Hillers et al. unpubl.	



Uganda	Uganda	Togo	Togo	Togo	Togo	Togo	Togo	Tanzania	Tanzania	Tanzania	Tanzania
Bwindi	Budongo	Yegué	Miassa Hohé	Kyabobo	Diguengué	Akloa	Usangu Wetlands	Usambara Mt	Uluguru Mts	Udzungwa	Serengeti
9	9	11	7	8	5	7	9	13	7	9	12
10	12	6	6	10	5	5	13	21	12	16	17
30	34	6	6	25	5	5	16	41	19	34	27
0	0	0	0	0	0	0	0	0	0	2	1
1	1	1	1	3	1	1	1	1	0	2	2
2	0	0	0	0	0	0	0	0	0	0	0
22	32	10	5	21	4	6	15	27	7	12	25
2	1	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	5	8	13	0
0	0	0	0	1	0	0	0	7	4	4	0
0	0	0	1	0	0	0	0	1	0	3	0
30	34	7	4	18	4	5	16	38	17	28	26
0	0	0	0	0	0	0	0	3	2	6	1
0	0	4	2	6	1	2	0	0	0	0	0
0	0	0	1	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
Drewes & Vindum 1994; Vonesh 2001	Auckland 1997; Schiøtz 1999	Hillers et al. 2009	Hillers et al. 2009	Rödel & Aguel 2003; Leaché et al. 2006	Hillers et al. 2009	Hillers et al. 2009	SMUWC 2001	cited in Vonesh 2001	Schiøtz 1981; Howell 1993	Menegon & Salvadio 2005; Burgess et al. 2007	Channing et al. 2004



Zambia	Zambia	Uganda	Uganda	Uganda	Uganda	Uganda
Northern Mwinilunge District	Lochinvar	Nabugabo	Mabira	Kyogo	Kibale	
10	8	9	7	8	9	
12	13	11	8	9	11	
31	18	23	12	18	33	
0	0	0	0	0	2	
2	0	0	0	0	2	
1	0	1	0	1	0	
28	18	22	12	17	29	
0	0	0	0	0	1	
0	0	0	0	0	1	
0	0	0	0	0	0	
0	0	0	0	0	0	
31	18	23	12	18	31	
0	0	0	0	0	2	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
0	0	0	0	0	0	
Broadley 1991	Simbotwe & Friend 1985	Behangana & Arusi 2004	Veith 2004	Behangana 2004	Vonesh 1998; 2001	



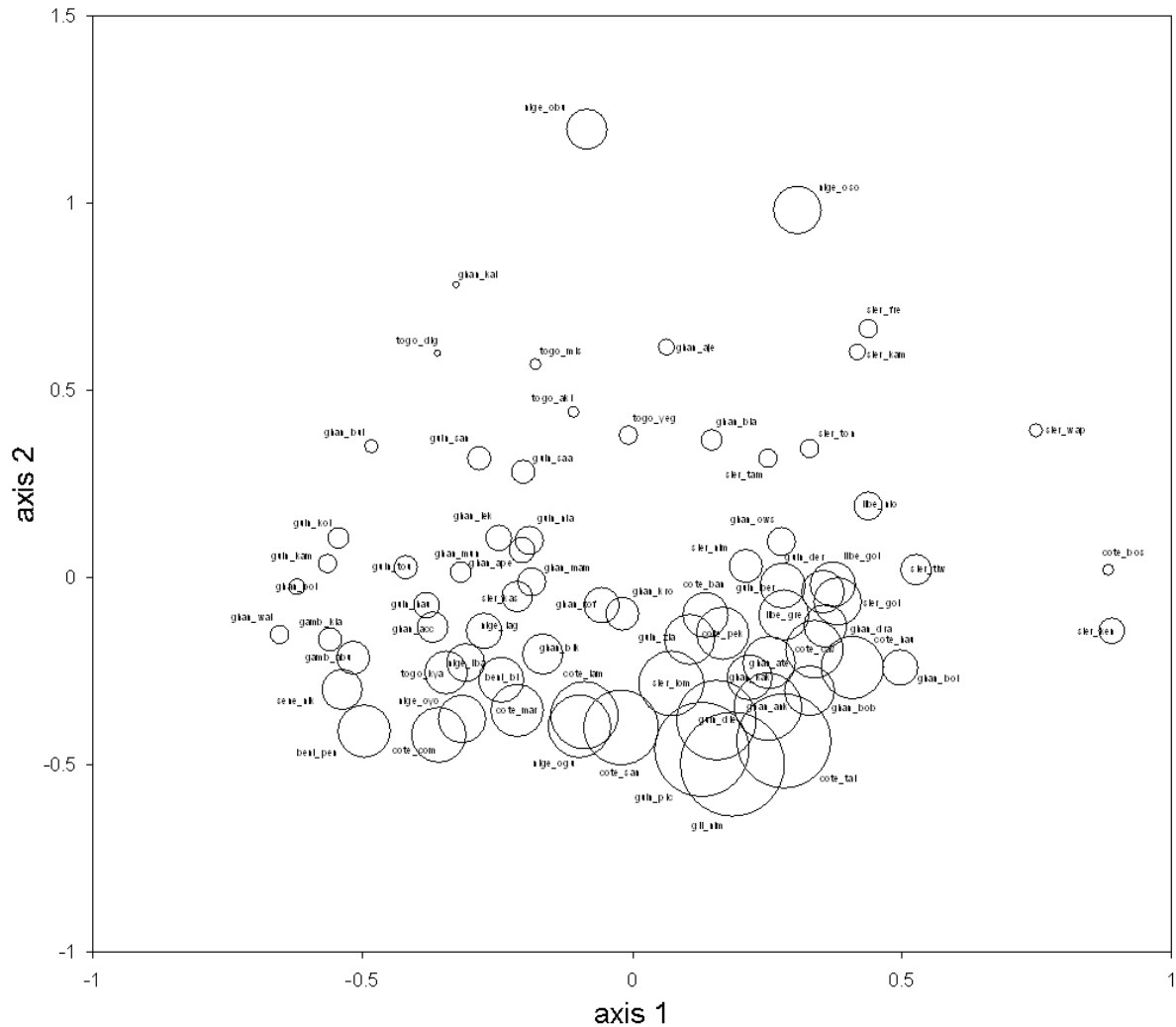
App. 3.2-2

Significance values for the fitted secondary matrices in the three NMDS sorted by the dissimilarity measure used. Only significant vectors are shown. The first five rows represent the habitat specificity of recorded species. The following six rows show the IUCN red list status of these species. The last 29 rows indicate their distribution within the proposed geographic barriers. Abbreviations are: (IUCN red list categories): not listed - NL; data deficient - DD; least concern - LC; near threatened - NT; vulnerable - VU; endangered - EN; critically endangered - CR; north west of Géba River - NW, Géba River - Ge, Kolenté River - Ko, Mano River - Ma, Cavally River - Ca, Banadama River (V Baolé) - Ba, Lake Volta - Vo, Dahomey Gap - Da, Niger River - Ni, Cross River - Cr, east of Cross River - RA.

	Jaccard			Raup-Crick			Mountford		
	R ²	p	Sig	R ²	p	Sig	R ²	p	Sig
forest	0.3023	< 0.0001	***	0.2815	< 0.0001	***	0.3172	< 0.0001	***
farmbush	0.181	0.0005	***	0.1915	0.0009	***	0.2134	< 0.0001	***
woodland	0.1393	0.0044	**	0.15	0.0036	**	0.229	< 0.0001	***
savannah	0.0992	0.0223	*	0.1507	0.0032	**	0.1816	0.0015	**
mont. grassland	0.2678	< 0.0001	***	0.2819	< 0.0001	***	0.2986	< 0.0001	***
NL	0.1379	0.0054	**	0.1316	0.007	**	0.178	0.0007	***
DD	0.0477	0.1728		0.0608	0.1109		0.0866	0.0358	*
NT	0.3442	< 0.0001	***	0.3475	< 0.0001	***	0.4123	< 0.0001	***
VU	0.0494	0.1591		0.0895	0.0371	*	0.0903	0.0342	*
EN	0.1062	0.0188	*	0.1239	0.0087	**	0.1765	0.001	***
RA	0.0086	0.713		0.2461	< 0.0001	***	0.2408	0.0003	***
Da - Vo	0.0592	0.1137		0.0441	0.1969		0.0822	0.0452	*
Vo - Ba	0.077	0.0623		0.1031	0.0236	*	0.2005	0.0008	***
Ca - Ma	0.0588	0.1208		0.0636	0.0986		0.1054	0.0189	*
Ma - Ko	0.1313	0.0081	**	0.1089	0.0234	*	0.1202	0.0099	**
RA - Ni	0.0949	0.0392	*	0.1429	0.0127	*	0.1455	< 0.0001	***
Vo - Ca	0.207	0.0004	***	0.2346	0.0002	***	0.295	< 0.0001	***
Ca - Ko	0.1041	0.0201	*	0.1272	0.0088	**	0.1768	0.0009	***
RA - Da	0.0362	0.2503		0.1877	0.0018	**	0.1639	0.0038	**
Vo - Ma	0.126	0.0073	**	0.1391	0.0048	**	0.2149	0.0002	***
Ba - Ko	0.4047	< 0.0001	***	0.4345	< 0.0001	***	0.446	< 0.0001	***
Ma - NW	0.1985	0.0005	***	0.236	< 0.0001	***	0.1696	0.0018	**
Ni - Da + Vo - Ma	0.1234	0.0082	**	0.1485	0.003	**	0.2437	< 0.0001	***
Vo - Ko	0.2861	< 0.0001	***	0.3349	< 0.0001	***	0.3763	< 0.0001	***
RA - Ba	0.1059	0.0183	*	0.0779	0.0557		0.2521	< 0.0001	***
RA - Da + Vo - Ca	0.0997	0.0207	*	0.1039	0.0182	*	0.0885	0.0376	*
RA - Ni + Vo - Ma	0.0898	0.0375	*	0.1071	0.0183	*	0.1487	0.004	**
Cr - Da + Vo - Ma	0.2224	< 0.0001	***	0.2168	0.0002	***	0.2123	0.0003	***
Ni - Da + Vo - Ko	0.3063	< 0.0001	***	0.3521	< 0.0001	***	0.424	< 0.0001	***
Da - Ko	0.102	0.0237	*	0.0775	0.057		0.1289	0.0073	**
Ba - NW	0.0723	0.068		0.0879	0.0376	*	0.0686	0.0762	
Ni - Ko	0.0945	0.0295	*	0.1268	0.0078	**	0.1619	0.0016	**
Da - Ge	0.1288	0.0092	**	0.15	0.0029	**	0.1849	0.0006	***
Vo - NW	0.1335	0.0069	**	0.186	0.0007	***	0.1374	0.0049	**
RA - Ma	0.1789	0.0007	***	0.2082	0.0004	***	0.3295	< 0.0001	***
RA - Da + Vo - Ko	0.2493	< 0.0001	***	0.2583	< 0.0001	***	0.2483	0.0002	***
RA - Ko	0.3234	< 0.0001	***	0.29	< 0.0001	***	0.295	< 0.0001	***
Cr - Ge	0.1765	0.0011	**	0.2009	0.0002	***	0.2975	0.0001	***
Ni - NW	0.2067	0.0001	***	0.2478	0.0002	***	0.2798	< 0.0001	***
Cr - NW	0.1422	0.0044	**	0.1152	0.0139	*	0.2677	< 0.0001	***

App. 3.2-3

NMDS of two axes of the West African assemblages. The sizes of the circles depicting the communities are drawn according to their respective species richness. Axis 1 separates communities by species habitat specificity, with rainforest dominated assemblages to the right and savannah dominated assemblages on the left. Axis 2 separates assemblages by species distributions, with sites containing local endemics on the bottom and sites containing widespread and Central African species on the top.





App. 3.3

App. 3.3-1

List of West African caecilian and anuran species tested for the presence of *Bd*, and their main ecological characters. All tests provided negative results. * = taxa known to comprise complexes of cryptic species (Rödel *et al.* unpubl. data); § = comprises 52 samples from Guinea (*N. o. occidentalis*) and 10 samples from Liberia (*N. o. liberiensis*); # = unknown species sampled at the airport in Accra, Ghana; swab = molecular investigation of swab sample; toe/skin = histological examination of toe tip; lowland = most populations below 1,500 m asl; montane = most populations above 1,500 m asl; forest = predominantly undisturbed evergreen rainforest; farmbush = degraded forest, open areas in rainforest, dry forest; savannah = tree and open savannah, agricultural land; tadpoles = aquatic feeding larvae; direct dev = direct development without free larval stage, either in egg (*Arthroleptis* spp., *Phrynobatrachus tokba*) or female (*Nimbaphrynoides*); lentic = larval development in stagnant, usually temporary waters of varying sizes; lotic = larval development in flowing, usually permanent waters of varying sizes. Taxonomy based on most recent list of the "Amphibian species of the World" (Frost 2011).

	sample		altitude		habitat			reproductive mode		breeding site	
	swab	toe/skin	lowland	montane	forest	farmbush	savannah	tadpoles	direct dev	lentic	lotic
Gymnophiona											
Caecilidae											
<i>Geotrypetes seraphini</i>	0	6	1	0	1	1	0	0	1	0	0
Anura											
Arthroleptidae											
<i>Arthroleptis</i> spp. *	24	0	1	0	1	1	0	0	1	0	0
<i>Astylosternus occidentalis</i>	3	0	1	0	1	1	0	1	0	0	1
<i>Cardioglossa occidentalis</i>	2	0	1	0	1	0	0	1	0	0	1
<i>Leptopelis spiritusnoctis</i>	5	0	1	0	1	1	0	1	0	1	0
<i>L. viridis</i>	8	0	1	0	0	1	1	1	0	1	0
Bufonidae											
<i>Amietophrynus maculatus</i>	17	0	1	0	0	1	1	1	0	1	0
<i>A. regularis</i>	1	0	1	0	0	1	1	1	0	1	0
<i>A. togoensis</i>	3	0	1	0	1	0	0	1	0	0	1
" <i>Bufo</i> " <i>pentoni</i>	4	0	1	0	0	0	1	1	0	1	0
<i>Nimbaphrynoides occidentalis</i> §	62	0	0	1	0	0	1	0	1	0	0
Dicroglossidae											
<i>Hoplobatrachus occipitalis</i>	55	12	1	0	0	1	1	1	0	1	0
Hemisotidae											
<i>Hemisus marmoratus</i>	5	0	1	0	1	1	1	1	0	1	0
Hyperoliidae											
<i>Afraxalus dorsalis</i>	3	0	1	0	0	1	1	1	0	1	0
<i>Afraxalus nigeriensis</i>	1	0	1	0	1	1	0	1	0	1	0
<i>Afraxalus vittiger</i>	5	0	1	0	0	0	1	1	0	1	0
<i>A. weidholzi</i>	1	0	1	0	0	0	1	1	0	1	0
<i>Hyperolius bobirensis</i>	2	0	1	0	1	0	0	1	0	1	0
<i>H. concolor</i>	5	0	1	0	0	1	0	1	0	1	0
<i>H. fusciventris</i>	1	0	1	0	1	1	0	1	0	1	0
<i>H. guttulatus</i>	2	0	1	0	0	1	0	1	0	1	0
<i>H. nasutus</i> *	1	0	1	0	0	0	1	1	0	1	0
<i>H. nitidulus</i>	6	0	1	0	0	0	1	1	0	1	0
<i>H. picturatus</i>	2	0	1	0	0	1	0	1	0	1	0
<i>H. sylvaticus</i>	2	0	1	0	1	0	0	1	0	1	0
<i>H. sp. #</i>	9	0	1	0	?	?	?	1	0	1	0
<i>Kassina arboricola</i>	2	0	1	0	1	1	0	1	0	1	0
<i>K. cassinoides</i>	2	0	1	0	0	0	1	1	0	1	0



<i>K. schioetzi</i>	3	0	1	0	0	1	1	0	0	1	0
<i>K. senegalensis</i>	12	0	1	0	0	0	1	1	0	1	0
<i>Phlyctimantis boulengeri</i>	2	0	1	0	1	1	0	1	0	1	0
Microhylidae											
<i>Phrynomantis microps</i>	33	0	1	0	0	0	1	1	0	1	0
Petropedetidae											
<i>Conraua alleni</i> *	52	34	1	1	1	0	0	1	0	0	1
<i>C. derooi</i>	5	7	1	0	1	0	0	1	0	0	1
<i>Petropedetes natator</i> *	138	20	1	1	1	0	0	1	0	0	1
Phrynobatrachidae											
<i>Phrynobatrachus alleni</i>	10	0	1	0	1	0	0	1	0	1	1
<i>P. annulatus</i>	9	0	1	0	1	0	0	?	?	?	?
<i>P. calcaratus</i> *	10	0	1	0	1	1	0	1	0	1	1
<i>P. francisci</i>	2	0	1	0	0	0	1	1	0	1	0
<i>P. latifrons</i>	43	36	1	0	0	1	1	1	0	1	0
<i>P. liberiensis</i>	19	0	1	0	1	0	0	1	0	0	1
<i>P. natalensis</i>	4	0	1	0	0	1	1	1	0	1	0
<i>P. plicatus</i>	19	0	1	0	1	0	0	1	0	1	0
<i>P. tokba</i>	2	0	1	1	1	1	0	0	1	0	0
<i>P. sp.</i>	1	0	1	0	?	?	?	?	?	?	?
Pipidae											
<i>Pseudhymenochirus merlini</i>	0	1	1	0	1	1	0	1	0	1	0
<i>Silurana tropicalis</i>	6	9	1	0	1	1	0	1	0	1	0
<i>Xenopus muelleri</i>	2	5	1	0	0	0	1	1	0	1	0
Ptychadenidae											
<i>Ptychadena aequiplicata</i> *	5	0	1	0	1	0	0	1	0	1	0
<i>P. bibroni</i>	1	0	1	0	0	1	1	1	0	1	0
<i>P. longirostris</i>	5	0	1	0	1	0	0	1	0	1	0
<i>P. mascareniensis</i> *	1	0	1	0	0	1	1	1	0	0	1
<i>P. oxyrhynchus</i>	1	0	1	0	0	1	1	1	0	1	0
<i>P. pumilio</i>	5	0	1	0	0	0	1	1	0	1	0
<i>P. tellini</i>	4	0	1	0	0	0	1	1	0	1	0
<i>P. tournieri</i>	2	0	1	0	0	0	1	1	0	1	0
Pyxicephalidae											
<i>Pyxicephalus edulis</i>	5	0	1	0	0	0	1	1	0	1	0
<i>Aubria subsigillata</i>	2	7	1	0	1	0	0	1	0	1	1
Ranidae											
<i>Hylarana albolabris</i>	11	0	1	0	1	0	0	1	0	0	1
<i>H. galamensis</i>	6	0	1	0	0	0	0	1	0	1	0
<i>H. occidentalis</i>	2	0	1	0	1	0	0	1	0	?	?
Rhacophoridae											
<i>Chiromantis rufescens</i>	1	0	1	0	1	0	0	1	0	1	0



App. 3.3-2

List of study areas, their geographic positions as well as details of sampling and analysis for each sample. The following abbreviations were used: CF = Classified Forest, FR = Forest Reserve, RR = Resource Reserve, NF = National Forest, NP = National Park, * = no coordinates available, species checked before exported alive; MfN = Museum fuer Naturkunde, NWU = North-Western University, UW = University of Washington, IoZ = Institute of Zoology. For columns N & O (controls) see text in material and method section.

Geographical details				Collection		Taxonomy		Sample sizes		Analyses				
Country	Site	Lat	Lon	Date(s)	Collector(s)	Family	Genus	Species	Swab	Toe/Skin	Lab(s)	Bd	ITS-4/5	Idn
Benin	Albani River Debochura, into Niger River	3.28	3.28	29.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	1	0	MfN	negative	NA	NA
Benin	Albani River Debochura, into Niger River	3.28	3.28	29.05.2009	Hirschfeld	Ranidae	<i>Hylarana</i>	<i>galamensis</i>	1	0	MfN	negative	NA	NA
Benin	Albani River Debochura, into Niger River	3.28	3.28	29.05.2009	Hirschfeld	Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>laurieri</i>	1	0	MfN	negative	NA	NA
Benin	Cotchi, Niger River	3.42		09.06.2009	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>torreiri</i>	1	0	MfN	negative	NA	NA
Benin	Goussoukrou, Albani River	3.13		31.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	1	0	MfN	negative	NA	NA
Benin	Kargi, Albani River	3.23		30.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	1	0	MfN	negative	NA	NA
Benin	Karimama	3.18		28.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	1	0	MfN	negative	NA	NA
Benin	Karimama	3.18		28.05.2009	Hirschfeld	Pipidae	<i>Xenopus</i>	<i>muelleri</i>	1	0	MfN	negative	NA	NA
Benin	Konfonon, Albani River	3.08		28.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	1	0	MfN	negative	NA	NA
Benin	Lokoli Forest, close to Koussiba	7.06	2.26	23.-24.5.2009	Nago, Brada, Schiefelhövel, Rödel	Ranidae	<i>Aubria</i>	<i>subsigillata</i>	0	1	NWU	negative	NA	NA
Benin	Lokoli Forest, close to Koussiba	7.06	2.26	23.-24.5.2009	Nago, Brada, Schiefelhövel, Rödel	Pipidae	<i>Silurana</i>	<i>occipitalis</i>	0	1	NWU	negative	NA	NA
Benin	Malaville	3.37		04.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	14	0	MfN	negative	NA	NA
Benin	Malaville	3.34		05.05. & 8.5.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	16	0	MfN	negative	NA	NA
Benin	Malaville	3.33		06.05.2009	Hirschfeld	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	2	0	MfN	negative	NA	NA
Benin	Malaville, Perimeter 1	3.37		04.05.2009	Hirschfeld	Ranidae	<i>Hylarana</i>	<i>galamensis</i>	2	0	MfN	negative	NA	NA
Benin	Monio	6.66	1.75	Nov. 2003	Montiz	Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>laurieri</i>	0	1	NWU	negative	NA	NA
Benin	Oueme Delta	6.58	2.52	20.11.2003	Montiz	Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>laurieri</i>	0	1	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Bufoidea	"Bulo"	<i>gambouzi</i>	4	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Hyperolidae	<i>Afrilus</i>	<i>vitiger</i>	3	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Hyperolidae	<i>Afrilus</i>	<i>vitiger</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Bufoidea	<i>Amietophrynus</i>	<i>marulatus</i>	8	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008 / Oct. 2003, Jan. 2004, 2.9.2004	Hirschfeld (3) / Grell (2), Montiz (2), Nago & Rödel (1)	Dicroglossidae	<i>Hoplobatrachus</i>	<i>occipitalis</i>	3	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Hyperolidae	<i>Kassina</i>	<i>caucasioides</i>	2	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Arthroleptidae	<i>Leptopelis</i>	<i>viridis</i>	4	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008 / 02.09.2004	Hirschfeld (32) / Nago & Rödel (1)	Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>laurieri</i>	32	1	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>laurieri</i>	4	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Microhylidae	<i>Phrynomantis</i>	<i>microgus</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	2	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	3	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>	1	0	NWU	negative	NA	NA
Benin	Pendani NP	1.40		rainy season 2008	Hirschfeld	Pyrrhonomidae	<i>Pyrrhonomus</i>	<i>laurieri</i>						

146



App. 3.3-3

List of positive African *Bd* records. The list shows localities which were accurate on the 30 arc sec grid. Out of the first 177 points 112 points were used for the ENMs (the remaining 65 fell on the same grid cell as another positive record). Record numbers 178 to 180 show the old records which are depicted in the figures but not used for the ENMs. The following abbreviation was used: NP = National Park. Taxonomy adjusted to most recent list of the "Amphibian species of the World" (Frost 2011) with original names in brackets.

No.	Country	Site	Lat	Lon	Genus	Species	Reference
1	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Afraxalus</i>	<i>paradorsalis</i>	1
2	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Hylarana</i> (<i>Amnirana</i>)	sp.	1
3	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Hylarana</i> (<i>Amnirana</i>)	sp.	1
4	Gabon	Monts de Cristal & Ivindo NP	0.52	12.79	<i>Hylarana</i> (<i>Amnirana</i>)	sp.	1
5	Gabon	Monts de Cristal & Ivindo NP	0.50	12.80	<i>Hylarana</i> (<i>Amnirana</i>)	sp.	1
6	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Arthroleptis</i>	sp.	1
7	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Arthroleptis</i>	sp.	1
8	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Cardioglossa</i>	<i>elegans</i>	1
9	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Chiromantis</i>	<i>rufescens</i>	1
10	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Chiromantis</i>	<i>rufescens</i>	1
11	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Chiromantis</i>	<i>rufescens</i>	1
12	Gabon	Monts de Cristal & Ivindo NP	0.50	12.79	<i>Conraua</i>	<i>crassipes</i>	1
13	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Hyperolius</i>	<i>ocellatus</i>	1
14	Gabon	Monts de Cristal & Ivindo NP	0.52	12.79	<i>Hyperolius</i>	<i>ocellatus</i>	1
15	Gabon	Monts de Cristal & Ivindo NP	0.50	12.79	<i>Hyperolius</i>	<i>ocellatus</i>	1
16	Gabon	Monts de Cristal & Ivindo NP	0.50	12.80	<i>Hyperolius</i>	<i>ocellatus</i>	1
17	Gabon	Monts de Cristal & Ivindo NP	0.62	10.41	<i>Hyperolius</i>	<i>tuberculatus</i>	1
18	Gabon	Monts de Cristal & Ivindo NP	0.50	12.79	<i>Leptopelis</i>	<i>aubryi</i>	1
19	Gabon	Monts de Cristal & Ivindo NP	0.50	12.79	<i>Leptopelis</i>	<i>aubryi</i>	1
20	Gabon	Monts de Cristal & Ivindo NP	0.50	12.80	<i>Leptopelis</i>	<i>aubryi</i>	1
21	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Leptopelis</i>	<i>brevirostris</i>	1
22	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Leptopelis</i>	<i>crystallinoron</i>	1
23	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Leptopelis</i>	<i>crystallinoron</i>	1
24	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Leptopelis</i>	<i>millsoni</i>	1
25	Gabon	Monts de Cristal & Ivindo NP	0.62	10.40	<i>Leptopelis</i>	sp.	1
26	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Leptopelis</i>	sp.	1
27	Gabon	Monts de Cristal & Ivindo NP	0.50	12.80	<i>Leptopelis</i>	sp.	1
28	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Petropedetes</i>	<i>vulpiae</i> (<i>newtoni</i>)	1
29	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Petropedetes</i>	<i>palmipes</i>	1
30	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Petropedetes</i>	<i>palmipes</i>	1
31	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Phrynobatrachus</i>	<i>auritus</i>	1
32	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Phrynobatrachus</i>	<i>auritus</i>	1
33	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Phrynobatrachus</i>	<i>auritus</i>	1
34	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Ptychadena</i>	sp.	1
35	Gabon	Monts de Cristal & Ivindo NP	0.50	12.79	<i>Ptychadena</i>	sp.	1
36	Gabon	Monts de Cristal & Ivindo NP	0.45	10.28	<i>Scotobleps</i>	<i>gabonicus</i>	1
37	Gabon	Monts de Cristal & Ivindo NP	0.63	10.40	<i>Scotobleps</i>	<i>gabonicus</i>	1
38	Gabon	Monts de Cristal & Ivindo NP	0.62	10.41	<i>Scotobleps</i>	<i>gabonicus</i>	1
39	Gabon	Monts de Cristal & Ivindo NP	0.51	12.80	<i>Afraxalus</i>	<i>fulvovittatus</i>	1
40	Kenya	Langata, Nairobi	-1.40	36.77	<i>Ptychadena</i>	<i>anchietae</i>	2
41	Malawi	Mulanje	-16.02	35.50	<i>Afraxalus</i>	<i>aureus</i> <i>crotalus</i>	3
42	Malawi	Mulanje	-16.02	35.52	<i>Amietia</i>	<i>angolensis</i>	3
43	Malawi	Mulanje	-15.90	35.67	<i>Amietia</i>	<i>angolensis</i>	3
44	Malawi	Mulanje	-15.96	35.69	<i>Amietia</i>	<i>angolensis</i>	3
45	Malawi	Mulanje	-15.96	35.69	<i>Amietia</i>	<i>angolensis</i>	3
46	Malawi	Mulanje	-15.96	35.69	<i>Amietia</i>	<i>johnstoni</i>	3
47	Malawi	Mulanje	-15.96	35.69	<i>Amietia</i>	<i>johnstoni</i>	3
48	Malawi	Mulanje	-15.82	35.72	<i>Arthroleptis</i>	<i>xenodactyloides</i>	3
49	Malawi	Mulanje	-15.82	35.72	<i>Arthroleptis</i>	<i>xenodactyloides</i>	3
50	Malawi	Mulanje	-15.89	35.62	<i>Nothophryne</i>	<i>broadleyi</i>	3



51	Malawi	Mulanje	-16.02	35.52	<i>Phrynobatrachus</i>	<i>natalensis</i>	3
52	Malawi	Mulanje	-15.82	35.72	<i>Phrynobatrachus</i>	<i>natalensis</i>	3
53	Malawi	Mulanje	-15.93	35.68	<i>Strongylopus</i>	<i>fuelleborni</i>	3
54	Malawi	Mulanje	-16.02	35.50	<i>Xenopus</i>	<i>muelleri</i>	3
55	Morocco	Agnane, Near Tetouan	35.54	-5.39	<i>Discoglossus</i>	<i>scovazzi</i>	4
56	Morocco	20km from Larache-Lakslakbir	35.04	-6.05	<i>Discoglossus</i>	<i>scovazzi</i>	4
57	Morocco	20km from Larache-Lakslakbir	35.04	-6.05	<i>Hyla</i>	<i>meridionalis</i>	4
58	Morocco	Larache	35.04	-6.03	<i>Pelobates</i>	<i>varavaldii</i>	4
59	DR Congo	Kahuzi Biega NP	-2.31	28.76	<i>Hyperolius</i>	<i>kivuensis</i>	5
60	DR Congo	Kahuzi Biega NP	-1.89	28.45	<i>Hyperolius</i>	<i>kuligae</i>	5
61	South Africa	Algeria, Cederberg	-32.37	19.06	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
62	South Africa	Bloukikerboom-water, Geogap	-29.63	18.01	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
63	South Africa	Grobbelaars River	-33.42	22.24	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
64	South Africa	Groot Winterhoek	-33.00	19.06	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
65	South Africa	Jamaka farm pond. Cederberg	-32.34	19.02	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
66	South Africa	Kraaifontein, Geogap	-29.63	18.03	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
67	South Africa	Stellenbosch	-33.93	18.87	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
68	South Africa	Swellendam	-34.01	20.46	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
69	South Africa	Table Mountain	-33.95	18.43	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
70	South Africa	Table Mountain	-33.95	18.43	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
71	South Africa	Tradouws pass	-33.97	20.70	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	6
72	South Africa	Jamaka farm pond. Cederberg	-32.34	19.02	<i>Strongylopus</i>	<i>grayii</i>	6
73	Lesotho	Katsi Dam	-29.34	28.51	<i>Amietia (Afrana)</i>	<i>dracomontana</i>	7
74	South Africa	Kammieskroon, Northern Cape	-30.2	17.93	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	7
75	South Africa	Springbok, Northern Cape	-26.85	21.78	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	7
76	Lesotho	Katsi Dam	-29.34	28.51	<i>Amietia</i>	<i>vertebralis</i>	7
77	South Africa	Springbok, Northern Cape	-26.85	21.78	<i>Vandijkophrynus (Bufo)</i>	<i>robinsoni</i>	7
78	South Africa	Kenton on Sea	-33.70	26.68	<i>Cacosternum</i>	<i>boettgeri</i>	7
79	South Africa	Oudtshoorn	-33.58	22.20	<i>Heleophryne</i>	<i>regis</i>	7
80	South Africa	Kenton on Sea	-33.70	26.68	<i>Kassina</i>	<i>senegalensis</i>	7
81	South Africa	Kenton on Sea	-33.70	26.68	<i>Strongylopus</i>	<i>fasciatus</i>	7
82	South Africa	Zeekoevlei, Western Cape	-34.07	18.52	<i>Xenopus</i>	<i>gilli</i>	7
83	Botswana	Kanye Youth Centre	-24.98	25.35	<i>Xenopus</i>	<i>laevis</i>	7
84	South Africa	Florisbad, Free State	-28.77	26.08	<i>Xenopus</i>	<i>laevis</i>	7
85	South Africa	Harrismith, Free State	-28.28	29.13	<i>Xenopus</i>	<i>laevis</i>	7
86	South Africa	Klapmuts	-33.81	18.86	<i>Xenopus</i>	<i>laevis</i>	7
87	South Africa	Koffiefontein	-29.40	25.02	<i>Xenopus</i>	<i>laevis</i>	7
88	South Africa	Kwa-Zulu, Natal	-30.98	29.23	<i>Xenopus</i>	<i>laevis</i>	7
89	South Africa	Sannaspos	-29.15	26.53	<i>Xenopus</i>	<i>laevis</i>	7
90	South Africa	Strand	-34.12	18.83	<i>Xenopus</i>	<i>laevis</i>	7
91	South Africa	Zeekoevlei, Western Cape	-34.07	18.52	<i>Xenopus</i>	<i>laevis</i>	7
92	Zambia	Lusaka	-15.02	28.23	<i>Xenopus</i>	<i>laevis</i>	7
93	Zambia	Lusaka	-15.02	28.23	<i>Xenopus</i>	<i>laevis</i>	7
94	Nigeria	Okomu National Park	6.30	5.25	<i>Chiromatis</i>	<i>rufescens</i>	8
95	Kenya	Mt. Elgon NP	1.03	34.77	NA	NA	9
96	Kenya	Saiwa Swamp NP	1.11	35.12	NA	NA	9
97	Kenya	Shimba Hills NP	-4.18	39.42	NA	NA	9
98	Kenya	Taita Hills (Mwatate)	-3.51	38.38	NA	NA	9
99	Kenya	Taita Hills (Mwundanyi)	-3.41	38.36	NA	NA	9
100	Kenya	Aberdares NP (moorlands)	-0.41	36.72	NA	NA	9
101	Kenya	Aberdares NP (Salient)	-0.37	36.84	NA	NA	9
102	Kenya	Kakamega Forest NP	0.35	34.87	NA	NA	9
103	Kenya	Nairobi (Karens)	-1.33	36.80	NA	NA	9
104	Kenya	Thompson Falls	0.04	36.37	NA	NA	9
105	Kenya	Tigoni Dam	-1.14	36.68	NA	NA	9
106	South Africa	Stutterheim, Kologha Forest	-32.54	27.37	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	10
107	South Africa	Grabouw	-34.15	19.02	<i>Xenopus</i>	<i>laevis</i>	11
108	South Africa	Bredasor/Bredasdorp?	-34.53	20.03	<i>Xenopus</i>	<i>laevis</i>	11
109	South Africa	Hex River	-33.48	19.58	<i>Xenopus</i>	<i>laevis</i>	11
110	South Africa	Knysna	-34.03	23.03	<i>Xenopus</i>	<i>laevis</i>	11
111	Nigeria	Kwano Camp (Gashaka Gumti NP)	7.33	11.59	<i>Amietophrynus</i>	sp.	12



112	Nigeria	Kwano Camp (Gashaka Gumti NP)	7.33	11.59	<i>Astylosternus</i>	sp.	12
113	Nigeria	Kwano Camp (Gashaka Gumti NP)	7.33	11.59	<i>Petropedetes</i>	sp.	12
114	Tanzania	Kihansi falls	-8.59	35.85	<i>Nectophrynoides</i>	<i>asperginis</i>	13
115	South Africa	Bela-Bela, Limpopo Province	-24.88	28.29	<i>Amietia (Afrana)</i>	<i>angolensis</i>	14
116	South Africa	Port Elizabeth, Eastern Cape	-33.97	25.58	<i>Amietia (Afrana)</i>	<i>fuscigula</i>	14
117	South Africa	Bela-Bela, Limpopo Province	-24.88	28.29	<i>Tomopterna</i>	<i>cryptotis</i>	14
118	South Africa	Bela-Bela, Limpopo Province	-24.88	28.29	<i>Tomopterna</i>	<i>natalensis</i>	14
119	South Africa	Botrivier, Western Cape	-34.23	19.20	<i>Xenopus</i>	<i>laevis</i>	14
120	South Africa	Wellington, Western Cape	-33.63	19.00	<i>Xenopus</i>	<i>laevis</i>	14
121	South Africa	Kommissiepoort, Free State	-29.32	27.28	<i>Xenopus</i>	<i>laevis</i>	15
122	South Africa	Moi River, KwaZulu-Natal	-29.20	29.98	<i>Xenopus</i>	<i>laevis</i>	15
123	South Africa	Phillipi, Western Cape	-34.02	18.55	<i>Xenopus</i>	<i>laevis</i>	15
124	South Africa	Rosendal, Free State	-28.52	27.93	<i>Xenopus</i>	<i>laevis</i>	15
125	South Africa	Windsorton Road, Northern Cape	-28.35	24.82	<i>Xenopus</i>	<i>laevis</i>	15
126	Cameroon	Ngoum-Bandi (PK27)	2.14	15.66	<i>Phlyctimantis</i>	<i>boulengeri</i>	16
127	Cameroon	Mt Oku	6.22	10.39	NA	NA	17
128	Cameroon	Bangabakundu	4.41	9.45	NA	NA	17
129	Cameroon	Mt Oku	6.25	10.52	NA	NA	17
130	Cameroon	Mt Oku	6.19	10.46	NA	NA	17
131	Cameroon	Mt Oku	6.19	10.46	NA	NA	17
132	Cameroon	Mt Cameroon	4.18	9.20	NA	NA	17
133	Cameroon	Mt Oku	6.24	10.52	NA	NA	17
134	Cameroon	Mt Oku	6.21	10.46	NA	NA	17
135	Cameroon	Mundame	4.56	9.52	NA	NA	17
136	Cameroon	Ndikinime	4.75	10.82	NA	NA	17
137	Cameroon	Ndikinime	4.75	10.83	NA	NA	17
138	Cameroon	Ndikinime	4.76	10.81	NA	NA	17
139	Cameroon	Mt Oku	6.20	10.46	NA	NA	17
140	Cameroon	Ntengue	5.37	10.02	NA	NA	17
141	Cameroon	Manengouba village	4.86	9.86	<i>Cardioglossa</i>	<i>melanogaster</i>	17
142	Cameroon	Manengouba village	4.96	9.87	<i>Leptodactylodon</i>	<i>mertensi</i>	17
143	Cameroon	Manengouba village	4.96	9.87	<i>Leptopelis</i>	<i>calcaratus</i>	17
144	Cameroon	Manengouba village	4.95	9.88	<i>Phrynobatrachus</i>	<i>africanus</i>	17
145	Cameroon	Mt Manengouba	5.07	9.87	<i>Cardioglossa</i>	<i>gracilis</i>	17
146	Cameroon	Mt Manengouba	5.07	9.87	<i>Cardioglossa</i>	<i>gracilis</i>	17
147	Cameroon	Mt Manengouba	5.07	9.87	<i>Cardioglossa</i>	<i>gracilis</i>	17
148	Cameroon	Mt Manengouba	5.07	9.87	<i>Cardioglossa</i>	<i>gracilis</i>	17
149	Cameroon	Mt Manengouba	5.07	9.87	<i>Cardioglossa</i>	<i>melanogaster</i>	17
150	Cameroon	Mt Manengouba	5.04	9.86	<i>Arthroleptis</i>	<i>perreti</i>	17
151	Cameroon	Mt Manengouba	5.04	9.86	<i>Leptodactylodon</i>	<i>erythrogaster</i>	17
152	Cameroon	Ebonemin	5.01	9.77	<i>Leptopelis</i>	<i>brevirostris</i>	17
153	Cameroon	Ebonemin	5.01	9.77	<i>Chlorolius</i>	<i>koehleri</i>	17
154	Cameroon	Ebonemin	5.01	9.78	<i>Leptodactylodon</i>	<i>mertensi</i>	17
155	Cameroon	Ebonemin	5.02	9.76	<i>Leptopelis</i>	<i>calcaratus</i>	17
156	Cameroon	Nkack	5.04	9.77	<i>Arthroleptis</i>	<i>tuberosus</i>	17
157	Cameroon	Nkack	5.04	9.77	<i>Phrynobatrachus</i>	<i>cricogaster</i>	17
158	Cameroon	Mt Manengouba	5.01	9.82	<i>Leptodactylodon</i>	<i>erythrogaster</i>	17
159	Cameroon	Mt Manengouba	5.01	9.82	<i>Leptopelis</i>	<i>modestus</i>	17
160	Cameroon	Mt Manengouba	5.01	9.82	<i>Arthroleptis</i>	<i>perreti</i>	17
161	Cameroon	Mt Manengouba	5.01	9.82	<i>Arthroleptis</i>	<i>perreti</i>	17
162	Cameroon	Mt Manengouba	5.04	9.81	<i>Arthroleptis</i>	<i>perreti</i>	17
163	Cameroon	Mt Manengouba	5.03	9.81	<i>Leptodactylodon</i>	<i>erythrogaster</i>	17
164	Cameroon	Ebo Forest Reserve	4.35	10.23	<i>Cardioglossa</i>	<i>leucomystax</i>	17
165	Ethiopia	Shawe bridge	6.65	39.73	NA	NA	18
166	Ethiopia	Katcha	6.72	39.73	NA	NA	18
167	Ethiopia	Rira	6.76	39.73	NA	NA	18
168	Ethiopia	Fute	6.76	39.75	NA	NA	18
169	Ethiopia	Tulla Nigressa	6.78	39.75	NA	NA	18
170	Ethiopia	Bonga town	7.27	36.26	NA	NA	18
171	Ethiopia	Bonga stream	7.27	36.26	NA	NA	18
172	Ethiopia	Bonga marsh	7.25	36.26	NA	NA	18



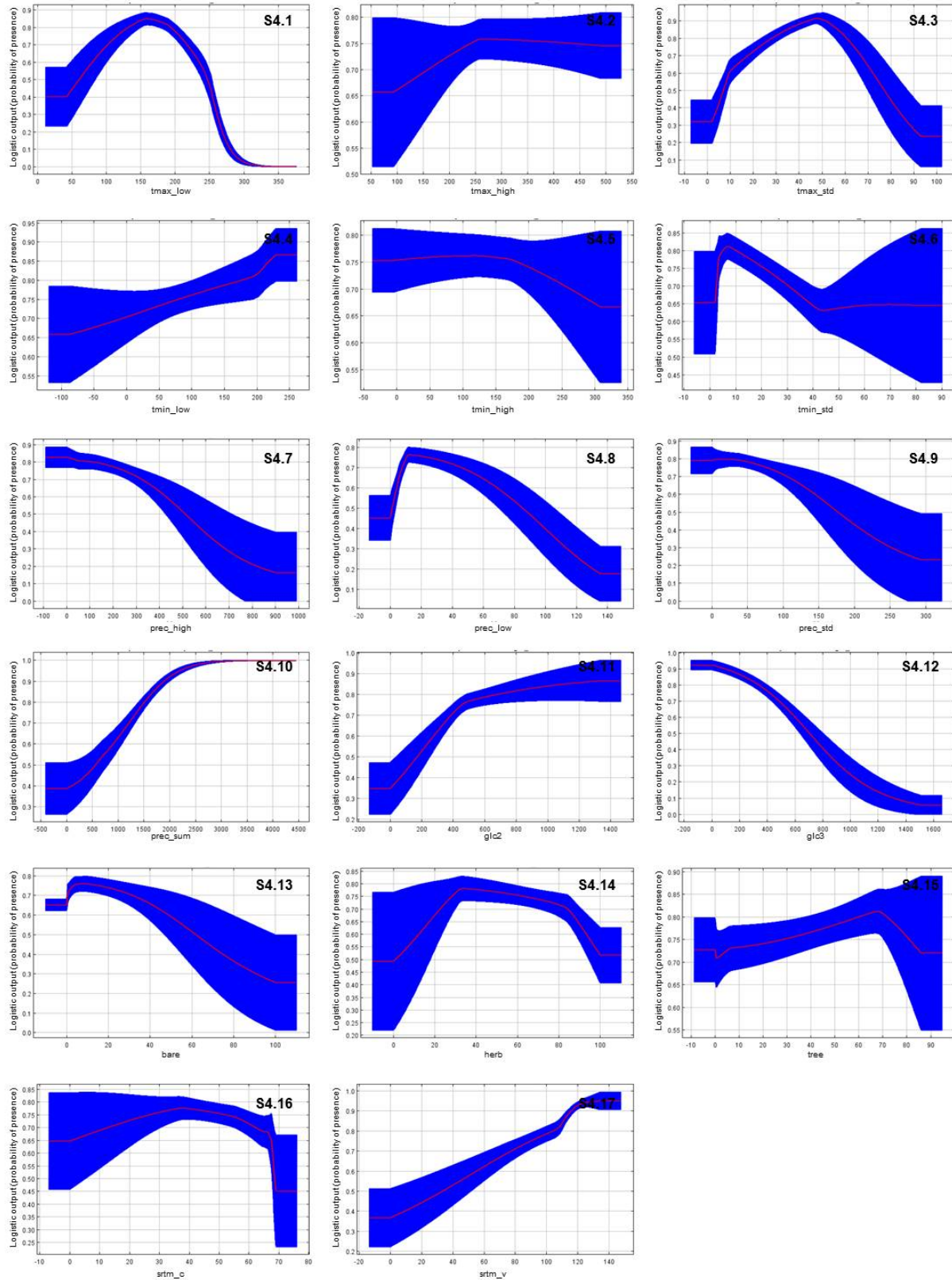
173	Ethiopia	Mankira	7.20	36.29	NA	NA	18
174	Ethiopia	Koma forest	7.32	36.08	NA	NA	18
175	Ethiopia	Koma marsh	7.31	36.08	NA	NA	18
176	Ethiopia	Wush wush	7.31	36.12	NA	NA	18
177	Ethiopia	Saja forest	7.49	36.09	NA	NA	18
178	Cameroon	Batouri District	4.43	14.34	<i>Xenopus</i>	<i>fraseri</i>	19
179	Uganda	Lake Bunyoni	-1.23	29.82	<i>Xenopus</i>	<i>laevis bunyoniensis</i>	19
180	Malawi	Lilongwe	-13.98	33.78	<i>Xenopus</i>	<i>laevis laevis</i>	19

References (abbreviated, see bibliography for full reference)

Bell *et al.* (2011)
 Berger & Parker (1999)
 Conradie *et al.* (2011)
 El Mouden *et al.* (2011)
 Greenbaum *et al.* (2008)
 Hopkins & Channing (2003)
 Aanensen (2011)
 Imasuen *et al.* (2011)
 Kielgast *et al.* (2010)
 Lane *et al.* (2003)
 Mendez *et al.* (1999)
 Reeder *et al.* (2011)
 Weldon *et al.* (2007)
 Weldon (2005)
 Weldon *et al.* (2004)
 Baláz *et al.* (2012)
 Doherty-Bone *et al.* (2013)
 Gower DJ *et al.* (2012)
 Soto-Azat *et al.* (2010)

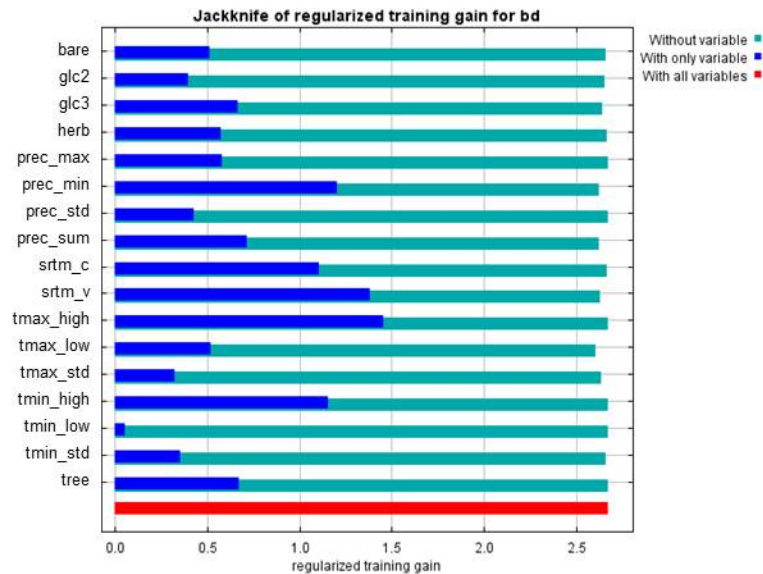
App. 3.3-4

Details of the variable contributions to the calculated ENMs. Figures S4.1 to S 4.17 show the mean individual response curves (red) and their standard deviation (blue). Figure S4.18 details the estimated relative variable contribution without (percentage contribution) and with random permutation (permutation importance) of the values. Figure S4.19 and S4.20 show the results of the jackknifing tests of variable importance for the training (S4.19) and testing data (S4.20).

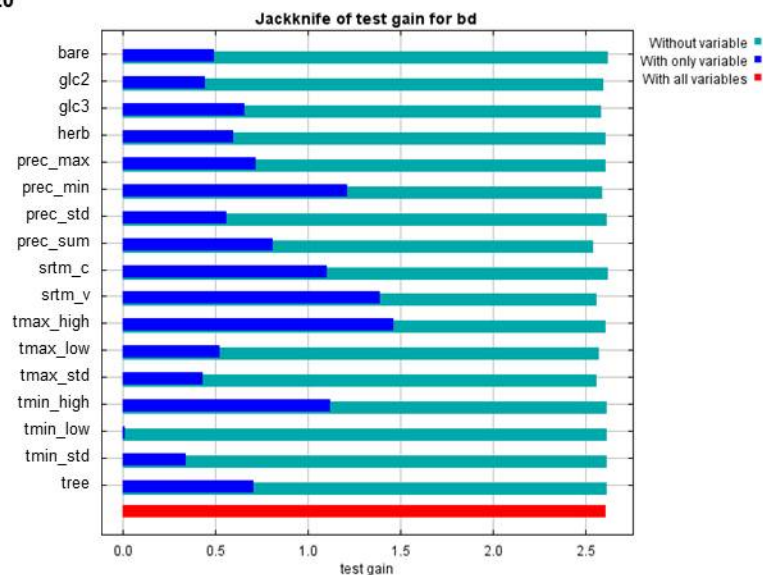


S4.18	Parameter	Percent contribution	Permutation importance
1	tmax_low	17.5	41.3
2	tmax_high	1.1	0.0
3	tmax_std	3.0	4.6
4	tmin_low	0.2	0.6
5	tmin_high	0.9	0.1
6	tmin_std	0.6	1.3
7	prec_high	0.1	1.2
8	prec_low	35.3	2.2
9	prec_std	0.2	1.0
10	prec_sum	5.0	12.3
11	glc2	0.5	1.5
12	glc3	1.3	11.8
13	bare	4.2	13.4
14	herb	3.2	3.9
15	tree	1.8	1.0
16	srtm_c	2.4	0.3
17	srtm_v	22.6	3.4

S4.19



S4.20





App. 3.4

App. 3.4.1-1

Main results from the individual ENMs per species.

Genus	Species	Regularized training gain	Unregularized training gain	Iterations	Training AUC
<i>Arthroleptis</i>	<i>aureoli</i>	4.0064	5.6494	120	0.9993
<i>Arthroleptis</i>	<i>brevipes</i>	4.8842	5.9025	280	0.9992
<i>Arthroleptis</i>	<i>crusculum</i>	4.9549	5.6217	480	0.9988
<i>Arthroleptis</i>	<i>formosus</i>	5.9725	7.22	240	0.9998
<i>Arthroleptis</i>	<i>krokosua</i>	5.8803	6.7924	140	0.9997
<i>Arthroleptis</i>	<i>langeri</i>	2.7989	4.12	100	0.9977
<i>Arthroleptis</i>	<i>nimbaensis</i>	1.9678	3.284	220	0.9953
<i>Arthroleptis</i>	<i>palava</i>	2.4032	3.8673	180	0.997
<i>Arthroleptis</i>	<i>poecilonotus</i>	2.5214	2.758	1880	0.9748
<i>Astylosternus</i>	<i>diadematus</i>	3.9261	4.6267	400	0.9976
<i>Astylosternus</i>	<i>montanus</i>	4.5814	5.3023	340	0.9985
<i>Astylosternus</i>	<i>occidentalis</i>	3.3921	3.5919	1820	0.9903
<i>Astylosternus</i>	<i>laticephalus</i>	2.2381	3.182	100	0.9919
<i>Cardioglossa</i>	<i>gracilis</i>	3.3871	3.7324	440	0.9911
<i>Cardioglossa</i>	<i>leucomystax</i>	2.8645	3.1729	480	0.9785
<i>Cardioglossa</i>	<i>melanogaster</i>	5.0026	5.4342	280	0.9985
<i>Cardioglossa</i>	<i>nigromaculata</i>	4.4454	5.2402	200	0.9983
<i>Cardioglossa</i>	<i>occidentalis</i>	3.7062	3.9282	1960	0.9928
<i>Cardioglossa</i>	<i>pulchra</i>	4.9979	5.6227	260	0.9988
<i>Cardioglossa</i>	<i>schioetzi</i>	4.5693	6.1338	140	0.9995
<i>Leptodactylodon</i>	<i>bicolor</i>	4.441	5.1364	260	0.9982
<i>Leptodactylodon</i>	<i>ovatus</i>	4.2401	4.9032	340	0.9978
<i>Leptodactylodon</i>	<i>polyacanthus</i>	3.9999	5.3691	100	0.9987
<i>Nyctibates</i>	<i>corrugatus</i>	4.3331	4.887	380	0.9979
<i>Scotoobleps</i>	<i>gabonicus</i>	3.462	3.7314	680	0.9902
<i>Trichobatrachus</i>	<i>robustus</i>	3.7811	3.9938	980	0.9932
<i>Leptopelis</i>	<i>aubryi</i>	2.2373	2.4783	500	0.9646
<i>Leptopelis</i>	<i>aubryioides</i>	2.8901	3.9397	220	0.9902
<i>Leptopelis</i>	<i>boulengeri</i>	3.2747	3.7071	540	0.9901
<i>Leptopelis</i>	<i>brevirostris</i>	3.5336	3.8681	460	0.9919
<i>Leptopelis</i>	<i>bufonides</i>	1.8267	2.5571	420	0.9728
<i>Leptopelis</i>	<i>calcaratus</i>	3.3312	3.6054	620	0.9853
<i>Leptopelis</i>	<i>macrotis</i>	3.5835	3.9437	680	0.9937
<i>Leptopelis</i>	<i>millsoni</i>	2.9109	3.278	380	0.9845
<i>Leptopelis</i>	<i>modestus</i>	4.5805	5.1083	300	0.9981
<i>Leptopelis</i>	<i>nordequatorialis</i>	3.4772	4.8453	240	0.9984
<i>Leptopelis</i>	<i>notatus</i>	2.2139	2.5802	340	0.9665
<i>Leptopelis</i>	<i>occidentalis</i>	3.7731	4.1961	440	0.9947
<i>Leptopelis</i>	<i>rufus</i>	3.7894	4.146	560	0.9932
<i>Leptopelis</i>	<i>spiritusnoctis</i>	2.5566	2.7212	1880	0.9767
<i>Leptopelis</i>	<i>viridis</i>	2.0845	2.2975	2260	0.9666
<i>Amietophrynus</i>	<i>camerunensis</i>	2.6444	2.9427	620	0.9791
<i>Amietophrynus</i>	<i>gracilipes</i>	2.6341	2.9675	400	0.9821
<i>Amietophrynus</i>	<i>maculatus</i>	1.2193	1.3631	1820	0.9075
<i>Amietophrynus</i>	<i>mauritanicus</i>	2.7951	3.1751	460	0.9854
<i>Amietophrynus</i>	<i>regularis</i>	1.1402	1.326	2780	0.9054
<i>Amietophrynus</i>	<i>superciliaris</i>				
<i>Amietophrynus</i>	<i>chevalieri</i>	3.1424	3.9511	360	0.9937
<i>Amietophrynus</i>	<i>superciliaris</i>				
<i>Amietophrynus</i>	<i>superciliaris</i>	2.9506	3.5413	620	0.9809
<i>Amietophrynus</i>	<i>taiensis</i>	2.855	3.8249	120	0.9961
<i>Amietophrynus</i>	<i>togoensis</i>	3.4308	3.6709	2060	0.9903
<i>Amietophrynus</i>	<i>xeros</i>	1.5745	1.9274	2480	0.9447
„Bufo“	<i>pentoni</i>	1.5943	2.1449	660	0.9618



<i>Didynamipus</i>	<i>sjostedti</i>	2.472	3.4708	100	0.9953
<i>Nectophryne</i>	<i>afra</i>	3.369	3.6676	500	0.9876
<i>Nimbaphrynoides</i>	<i>occidentalis</i>	5.727	6.001	300	0.9989
<i>Werneria</i>	<i>mertensiana</i>	3.5735	4.9277	160	0.9978
<i>Werneria</i>	<i>preussi</i>	5.1838	6.2163	120	0.9995
<i>Wolterstorffina</i>	<i>parvipalmata</i>	4.4765	4.844	300	0.9977
<i>Hoplobatrachus</i>	<i>occipitalis</i>	1.2973	1.4554	2120	0.9159
<i>Hemisus</i>	<i>guineensis</i>	1.3717	1.7089	660	0.915
<i>Hemisus</i>	<i>marmoratus</i>	1.2244	1.4267	2220	0.9109
<i>Acanthixalus</i>	<i>sonjae</i>	2.7483	3.8484	280	0.9958
<i>Acanthixalus</i>	<i>spinosus</i>	1.6529	2.403	180	0.9794
<i>Afixalus</i>	<i>dorsalis</i>	2.571	2.7481	1880	0.9775
<i>Afixalus</i>	<i>fulvovittatus</i>	2.8352	3.2511	1260	0.9839
<i>Afixalus</i>	<i>nigeriensis</i>	3.312	3.8318	660	0.9932
<i>Afixalus</i>	<i>paradorsalis</i>	3.5128	3.8052	380	0.9922
<i>Afixalus</i>	<i>quadrivittatus</i>	1.9296	2.2239	1940	0.9592
<i>Afixalus</i>	<i>vibekae</i>	2.043	2.832	160	0.9846
<i>Afixalus</i>	<i>vittiger</i>	2.5722	2.8875	2900	0.9814
<i>Afixalus</i>	<i>weidholzi</i>	1.8824	2.4332	900	0.9721
<i>Hyperolius</i>	<i>baumanni</i>	3.8203	4.4836	440	0.9956
<i>Hyperolius</i>	<i>bobirensis</i>	2.6306	3.4082	100	0.995
<i>Hyperolius</i>	<i>bolifambae</i>	3.2886	3.7803	440	0.9905
<i>Hyperolius</i>	<i>burtoni</i>	3.405	3.581	1160	0.9906
<i>Hyperolius</i>	<i>chlorosteus</i>	3.7005	3.9989	960	0.9937
<i>Hyperolius</i>	<i>concolor</i>	2.2353	2.4465	1940	0.9699
<i>Hyperolius</i>	<i>fusciventris</i>	3.724	3.9692	1580	0.9932
<i>Hyperolius</i>	<i>guttulatus</i>	2.9763	3.2312	1820	0.9869
<i>Hyperolius</i>	<i>igbettensis</i>	2.4447	2.8085	600	0.9769
<i>Hyperolius</i>	<i>koehleri</i>	2.8455	4.3693	140	0.997
<i>Hyperolius</i>	<i>lamottei</i>	3.1938	3.5706	540	0.9897
<i>Hyperolius</i>	<i>lamtoensis</i>	4.2649	5.1544	360	0.9989
<i>Hyperolius</i>	<i>laurenti</i>	3.6754	4.5592	360	0.9976
<i>Hyperolius</i>	<i>nienokouensis</i>	3.3485	4.281	140	0.9978
<i>Hyperolius</i>	<i>nimbae</i>	2.4164	3.5817	260	0.9954
<i>Hyperolius</i>	<i>nitidulus</i>	2.1097	2.4138	3240	0.9701
<i>Hyperolius</i>	<i>occidentalis</i>	3.5417	4.227	320	0.9952
<i>Hyperolius</i>	<i>ocellatus</i>	2.8424	3.0434	440	0.9783
<i>Hyperolius</i>	<i>picturatus</i>	3.0215	3.2419	1820	0.9868
<i>Hyperolius</i>	<i>riggenbachi</i>	3.7265	4.4591	460	0.9947
<i>Hyperolius</i>	<i>soror</i>	3.1121	4.0853	480	0.9966
<i>Hyperolius</i>	<i>spatzi</i>	3.1912	3.9647	560	0.9857
<i>Hyperolius</i>	<i>sylvaticus</i>	2.9576	3.3626	540	0.9886
<i>Hyperolius</i>	<i>torrentis</i>	4.165	5.2087	320	0.9985
<i>Hyperolius</i>	<i>tuberculatus</i>	2.3607	2.8194	480	0.9739
<i>Hyperolius</i>	<i>viridigulosus</i>	3.1673	4.2877	220	0.9961
<i>Hyperolius</i>	<i>zonatus</i>	3.4777	4.0624	460	0.9948
<i>Kassina</i>	<i>arboricola</i>	2.9853	3.8846	420	0.9956
<i>Kassina</i>	<i>cassinoides</i>	2.7362	3.3148	620	0.9805
<i>Kassina</i>	<i>cochranae</i>	3.4197	3.7988	740	0.9894
<i>Kassina</i>	<i>fusca</i>	2.429	2.8857	840	0.9805
<i>Kassina</i>	<i>lamottei</i>	3.15	4.6463	380	0.9983
<i>Kassina</i>	<i>schioetzi</i>	2.7025	3.8833	360	0.9965
<i>Kassina</i>	<i>senegalensis</i>	1.0292	1.1619	2240	0.8819
<i>Morerella</i>	<i>cyanophthalma</i>	4.7334	6.6819	320	0.9997
<i>Opisthothylax</i>	<i>immaculatus</i>	3.3326	3.809	600	0.9928
<i>Phlyctimantis</i>	<i>boulengeri</i>	3.3154	3.9185	640	0.993
<i>Phrynomantis</i>	<i>microps</i>	2.4394	2.7495	980	0.973
<i>Conraua</i>	<i>alleni</i> complex	3.7968	3.9604	1320	0.9928
<i>Conraua</i>	<i>alleni</i> complex	3.3574	4.7033	380	0.9982
<i>Conraua</i>	<i>crassipes</i>	3.0909	3.3842	660	0.9886
<i>Conraua</i>	<i>derooi</i>	1.6292	2.037	100	0.9628

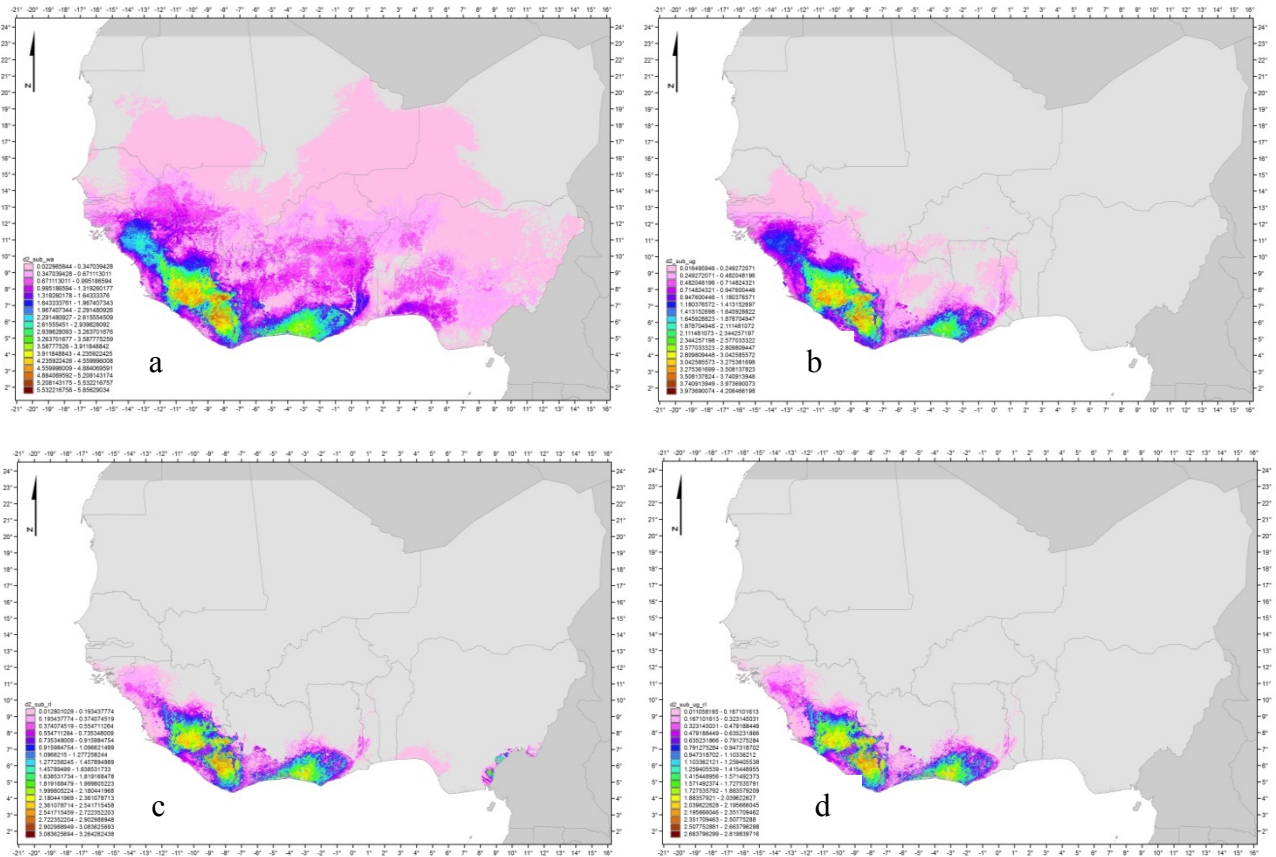


<i>Conraua</i>	<i>derooi</i>	3.9224	5.4357	300	0.9992
<i>Conraua</i>	<i>robusta</i>	4.5884	5.0665	360	0.998
<i>Petropedetes</i>	<i>cameronensis</i>	4.5551	4.9008	400	0.9956
<i>Petropedetes</i>	<i>parkeri</i>	3.9591	4.5685	300	0.9965
<i>Odontobatrachus</i>	<i>natator</i> complex	4.0081	4.3687	560	0.9959
<i>Odontobatrachus</i>	<i>natator</i> complex	4.7107	5.254	560	0.9984
<i>Odontobatrachus</i>	<i>natator</i> complex	2.9857	4.4454	120	0.9984
<i>Odontobatrachus</i>	<i>natator</i> complex	2.4158	3.1057	260	0.9956
<i>Odontobatrachus</i>	<i>natator</i> complex	4.5395	4.8575	600	0.9973
<i>Petropedetes</i>	<i>parkeri</i>	3.9591	4.5685	300	0.9965
<i>Phrynobatrachus</i>	<i>africanus</i>	3.4109	3.9759	480	0.9915
<i>Phrynobatrachus</i>	<i>alleni</i>	2.9831	3.1887	1680	0.9853
<i>Phrynobatrachus</i>	<i>annulatus</i>	3.7589	4.149	1100	0.993
<i>Phrynobatrachus</i>	<i>auritus</i>	2.7185	3.0587	1680	0.982
<i>Phrynobatrachus</i>	<i>batesii</i>	2.3809	3.1872	160	0.9843
<i>Phrynobatrachus</i>	<i>calcaratus</i>	2.6522	2.8353	1700	0.9783
<i>Phrynobatrachus</i>	<i>cricogaster</i>	4.6258	5.0956	180	0.9981
<i>Phrynobatrachus</i>	<i>francisci</i>	2.3281	2.6435	2180	0.9741
<i>Phrynobatrachus</i>	<i>fraterculus</i>	3.6653	3.9865	760	0.9938
<i>Phrynobatrachus</i>	<i>ghanensis</i>	4.2693	5.148	600	0.9983
<i>Phrynobatrachus</i>	<i>guineensis</i>	3.645	4.1028	540	0.9945
<i>Phrynobatrachus</i>	<i>gutturosus</i>	2.6222	2.9771	2820	0.982
<i>Phrynobatrachus</i>	<i>intermedius</i>	6.2167	7.2827	180	0.9998
<i>Phrynobatrachus</i>	<i>latifrons</i>	2.1448	2.3167	2100	0.9661
<i>Phrynobatrachus</i>	<i>liberiensis</i>	3.2333	3.4118	1640	0.9877
<i>Phrynobatrachus</i>	<i>natalensis</i>	0.9925	1.1233	2000	0.8839
<i>Phrynobatrachus</i>	<i>phyllophilus</i>	3.4574	3.6812	2120	0.9911
<i>Phrynobatrachus</i>	<i>plicatus</i>	3.0596	3.2679	1640	0.9865
<i>Phrynobatrachus</i>	<i>steindachneri</i>	4.4806	4.8522	420	0.9968
<i>Phrynobatrachus</i>	<i>tokba</i>	2.9009	3.0856	1520	0.9829
<i>Phrynobatrachus</i>	<i>villiersi</i>	3.6269	4.1234	760	0.9947
<i>Phrynobatrachus</i>	<i>wernerii</i>	4.3852	5.3441	140	0.9986
<i>Hymenochirus</i>	<i>boettgeri</i>	2.1303	2.5985	480	0.971
<i>Pseudhymenochirus</i>	<i>merlini</i>	2.6781	3.7763	140	0.9947
<i>Silurana</i>	<i>tropicalis</i>	2.2927	2.5297	2300	0.9722
<i>Xenopus</i>	<i>laevis</i>	1.6268	1.7601	1860	0.9329
<i>Xenopus</i>	<i>muelleri</i>	1.2622	1.5265	2720	0.9184
<i>Hildebrandtia</i>	<i>ornata</i>	1.1296	1.4236	420	0.902
<i>Ptychadena</i>	<i>aequiplicata</i> complex	2.7259	3.2047	500	0.9815
<i>Ptychadena</i>	<i>aequiplicata</i> complex	3.7446	4.0924	680	0.9942
<i>Ptychadena</i>	<i>aequiplicata</i> complex	3.6964	3.9616	620	0.9935
<i>Ptychadena</i>	<i>bibroni</i>	2.0632	2.2885	3080	0.965
<i>Ptychadena</i>	<i>longirostris</i>	2.8836	3.1199	1700	0.9847
<i>Ptychadena</i>	<i>mascareniensis</i> complex	1.1297	1.2985	2220	0.8986
<i>Ptychadena</i>	<i>oxyrhynchus</i>	1.2872	1.4632	2300	0.9148
<i>Ptychadena</i>	<i>pujoli</i>	1.1446	2.0245	80	0.9606
<i>Ptychadena</i>	<i>pumilio</i>	2.1707	2.3912	1860	0.9674
<i>Ptychadena</i>	<i>retropunctata</i>	3.9832	4.5759	400	0.9974
<i>Ptychadena</i>	<i>schillukorum</i>	1.1128	1.5467	320	0.9032
<i>Ptychadena</i>	<i>submascareniensis</i>	4.1765	4.718	540	0.9974
<i>Ptychadena</i>	<i>superciliaris</i>	3.2062	3.6595	420	0.9888
<i>Ptychadena</i>	<i>tellinii</i>	1.9374	2.2534	600	0.9605
<i>Ptychadena</i>	<i>tourneri</i>	2.5546	2.9877	1040	0.9775
<i>Ptychadena</i>	<i>trinodis</i>	1.819	2.1255	500	0.9507
<i>Aubria</i>	<i>subsagillata</i>	3.2066	3.4665	540	0.9882
<i>Tomopterna</i>	<i>cryptotis</i> complex	1.6866	2.406	160	0.9741
<i>Pyxicephalus</i>	<i>edulis</i>	1.6621	2.3738	220	0.9729
<i>Hylarana</i>	<i>albolabris</i>	1.895	2.0101	1580	0.952
<i>Hylarana</i>	<i>asperima</i>	4.2281	5.5796	200	0.9991
<i>Hylarana</i>	<i>galamensis</i>	1.6899	1.8998	1780	0.9429

<i>Hylarana</i>	<i>occidentalis</i>	4.001	4.4127	560	0.9963
<i>Chiromantis</i>	<i>rufescens</i>	2.7003	2.9016	1700	0.9801
<i>Geotrypetes</i>	<i>seraphini</i> complex	2.6549	3.1542	540	0.9839
<i>Herpele</i>	<i>squalostoma</i>	2.4294	3.3339	340	0.989

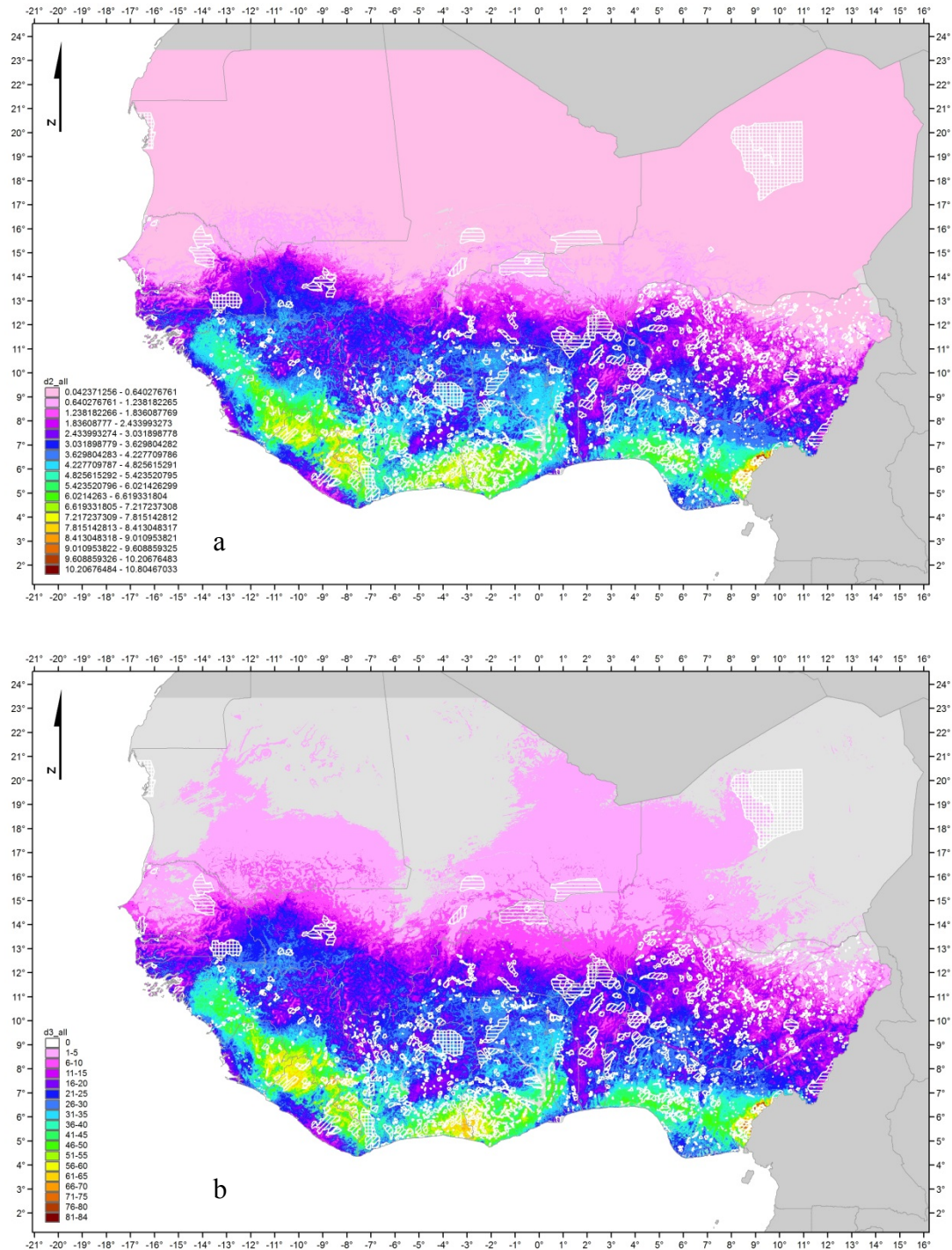
App. 3.4.1-2

Maps depicting modelled amphibian diversity (Shannon, see text) for different subsets: a) species endemic to West African; b) species endemic to Upper Guinea; c) species listed on the IUCN Red List as threatened; d) species endemic to Upper Guinea and listed on the IUCN Red List as threatened.



App. 3.4.1-3

Maps depicting the existing protected area network and modelled amphibian diversity (a; Shannon, see text) as well as binary species richness (b). The protected areas are coloured in white with the following categories: international = vertical lines, national IUCN I-VI = horizontal lines, national others = 45° lines. The latter include the so called "classified forests" ("forêts classées").





App. 3.4.2-1

Table listing all species and their ENM range sizes. The columns show from left to right: taxonomic order, family, species, species authority and the modelled range size in 30arc second grid cells which approximate to 1 km² (see text for details). Asterisks indicate valid candidate species (see Vieites *et al.* 2009).

Order	Family	Species	Authority	Modelled range-size
Anura	Arthroleptidae	<i>Arthroleptis aureoli</i>	(Schizt, 1964)	676
Anura	Arthroleptidae	<i>Arthroleptis brevipes</i>	Ahl, 1924	1,406
Anura	Arthroleptidae	<i>Arthroleptis cruscolum</i>	Angel, 1950	2,206
Anura	Arthroleptidae	<i>Arthroleptis formosus</i>	Rödel <i>et al.</i> , 2011	4,926
Anura	Arthroleptidae	<i>Arthroleptis krokosua</i>	Ernst <i>et al.</i> , 2008	357
Anura	Arthroleptidae	<i>Arthroleptis langeri</i>	Rödel <i>et al.</i> , 2009	762
Anura	Arthroleptidae	<i>Arthroleptis nimbaensis</i>	Angel, 1950	8,531
Anura	Arthroleptidae	<i>Arthroleptis palava</i>	Blackburn <i>et al.</i> , 2010	7,894
Anura	Arthroleptidae	<i>Arthroleptis poecilonotus</i>	Peters, 1863	1,908,154
Anura	Arthroleptidae	<i>Astylosternus diadematus</i>	Werner, 1898	68,805
Anura	Arthroleptidae	<i>Astylosternus laticephalus</i>	Rödel <i>et al.</i> , 2012	112,760
Anura	Arthroleptidae	<i>Astylosternus montanus</i>	Amiet, 1978	51,707
Anura	Arthroleptidae	<i>Astylosternus occidentalis</i>	Parker, 1931	144,078
Anura	Arthroleptidae	<i>Cardioglossa gracilis</i>	Boulenger, 1900	582,844
Anura	Arthroleptidae	<i>Cardioglossa leucomystax</i>	(Boulenger, 1903)	1,156,159
Anura	Arthroleptidae	<i>Cardioglossa melanogaster</i>	Amiet, 1972	9,987
Anura	Arthroleptidae	<i>Cardioglossa nigromaculata</i>	Nieden, 1908	49,790
Anura	Arthroleptidae	<i>Cardioglossa occidentalis</i>	Blackburn <i>et al.</i> , 2008	72,104
Anura	Arthroleptidae	<i>Cardioglossa pulchra</i>	Schizt, 1963	15,735
Anura	Arthroleptidae	<i>Cardioglossa schioetzi</i>	Amiet, 1982	5,347
Anura	Arthroleptidae	<i>Leptodactylodon bicolor</i>	Amiet, 1971	62,036
Anura	Arthroleptidae	<i>Leptodactylodon ovatus</i>	Andersson, 1903	64,011
Anura	Arthroleptidae	<i>Leptodactylodon polyacanthus</i>	Amiet, 1971	54,736
Anura	Arthroleptidae	<i>Leptopelis aubryi</i>	(Duméril, 1856)	1,967,010
Anura	Arthroleptidae	<i>Leptopelis aubryioides</i>	(Andersson, 1907)	541,668
Anura	Arthroleptidae	<i>Leptopelis boulengeri</i>	(Werner, 1898)	543,958
Anura	Arthroleptidae	<i>Leptopelis brevirostris</i>	(Werner, 1898)	236,334
Anura	Arthroleptidae	<i>Leptopelis bufonides</i>	Schizt, 1967	1,078,678
Anura	Arthroleptidae	<i>Leptopelis calcaratus</i>	(Boulenger, 1906)	682,284
Anura	Arthroleptidae	<i>Leptopelis macrotis</i>	Schizt, 1967	148,886
Anura	Arthroleptidae	<i>Leptopelis millsoni</i>	(Boulenger, 1895)	1,098,257
Anura	Arthroleptidae	<i>Leptopelis modestus</i>	(Werner, 1898)	38,796
Anura	Arthroleptidae	<i>Leptopelis nordequatorialis</i>	Perret, 1966	23,070
Anura	Arthroleptidae	<i>Leptopelis notatus</i>	(Peters, 1875)	2,527,551
Anura	Arthroleptidae	<i>Leptopelis occidentalis</i>	Schizt, 1967	111,843
Anura	Arthroleptidae	<i>Leptopelis rufus</i>	Reichenow, 1874	143,921
Anura	Arthroleptidae	<i>Leptopelis spiritusnoctis</i>	Rödel, 2007	479,238
Anura	Arthroleptidae	<i>Leptopelis viridis</i>	(Günther, 1869)	1,451,815
Anura	Arthroleptidae	<i>Nyctibates corrugatus</i>	Boulenger, 1904	95,171
Anura	Arthroleptidae	<i>Scotobleps gabonicus</i>	Boulenger, 1900	257,670
Anura	Arthroleptidae	<i>Trichobatrachus robustus</i>	Boulenger, 1900	120,128
Anura	Bufonidae	<i>"Bufo" pentoni</i>	Anderson, 1893	2,573,134
Anura	Bufonidae	<i>Amietophrynus camerunensis</i>	(Parker, 1936)	1,861,024
Anura	Bufonidae	<i>Amietophrynus gracilipes</i>	(Boulenger, 1899)	1,047,714
Anura	Bufonidae	<i>Amietophrynus maculatus</i>	(Hallowell, 1854)	7,351,517
Anura	Bufonidae	<i>Amietophrynus mauritanicus</i>	(Schlegel, 1841)	671,702
Anura	Bufonidae	<i>Amietophrynus regularis</i>	(Reuss, 1833)	6,070,549
Anura	Bufonidae	<i>Amietophrynus superciliaris chevalieri</i>	(Mocquard, 1908)	244,414
Anura	Bufonidae	<i>Amietophrynus superciliaris superciliaris</i>	(Boulenger, 1888)	830,429
Anura	Bufonidae	<i>Amietophrynus taiensis</i>	(Rödel & Ernst, 2000)	8,893
Anura	Bufonidae	<i>Amietophrynus togoensis</i>	(Ahl, 1924)	139,545
Anura	Bufonidae	<i>Amietophrynus xeros</i>	(Tandy <i>et al.</i> , 1976)	5,181,921
Anura	Bufonidae	<i>Didynamipus sjostedti</i>	Andersson, 1903	68,010



Anura	Bufonidae	<i>Nectophryne afra</i>	Buchholz & Peters, 1875	560,062
Anura	Bufonidae	<i>Nimbaphrynoides occidentalis</i>	(Angel, 1943)	142
Anura	Bufonidae	<i>Werneria mertensiana</i>	Amiet, 1976	71,611
Anura	Bufonidae	<i>Werneria preussi</i>	(Matschie, 1893)	6,437
Anura	Bufonidae	<i>Wolterstorffia parvipalmata</i>	(Werner, 1898)	46,113
Anura	Conrauidae	<i>Conraua alleni</i> 1	(Barbour & Loveridge, 1927)*	59,525
Anura	Conrauidae	<i>Conraua alleni</i> 2	(Barbour & Loveridge, 1927)*	64,517
Anura	Conrauidae	<i>Conraua crassipes</i>	(Buchholz & Peters, 1875)	606,480
Anura	Conrauidae	<i>Conraua derooi</i> 1	Huselmans, 1972*	2,153
Anura	Conrauidae	<i>Conraua derooi</i> 2	Huselmans, 1972*	3,471
Anura	Conrauidae	<i>Conraua robusta</i>	Nieden, 1908	53,676
Anura	Dicroglossidae	<i>Hoplobatrachus occipitalis</i>	(Günther, 1858)	5,647,905
Anura	Hemisotidae	<i>Hemisus guineensis</i>	Cope, 1865	6,118,856
Anura	Hemisotidae	<i>Hemisus marmoratus</i>	(Peters, 1854)	7,511,033
Anura	Hyperoliidae	<i>Acanthixalus sonjae</i>	Rödel <i>et al.</i> , 2003	126,322
Anura	Hyperoliidae	<i>Acanthixalus spinosus</i>	(Buchholz & Peters, 1875)	733,484
Anura	Hyperoliidae	<i>Afrixalus dorsalis</i>	(Peters, 1875)	685,950
Anura	Hyperoliidae	<i>Afrixalus fulvovittatus</i>	(Cope, 1861)	751,099
Anura	Hyperoliidae	<i>Afrixalus nigeriensis</i>	Schiøtz, 1863	264,539
Anura	Hyperoliidae	<i>Afrixalus paradorsalis</i>	Perret, 1960	347,116
Anura	Hyperoliidae	<i>Afrixalus quadrivittatus</i>	(Werner, 1908)	2,351,223
Anura	Hyperoliidae	<i>Afrixalus vibekae</i>	Schiøtz, 1967	170,872
Anura	Hyperoliidae	<i>Afrixalus vittiger</i>	(Peters, 1876)	889,515
Anura	Hyperoliidae	<i>Afrixalus weidholzi</i>	(Mertens, 1938)	1,466,063
Anura	Hyperoliidae	<i>Hyperolius baumanni</i>	Ahl, 1931	169,106
Anura	Hyperoliidae	<i>Hyperolius bobirensis</i>	Schiøtz, 1967	28,965
Anura	Hyperoliidae	<i>Hyperolius bolifambae</i>	Mertens, 1938	214,686
Anura	Hyperoliidae	<i>Hyperolius burtoni</i>	Noble, 1924*	333,720
Anura	Hyperoliidae	<i>Hyperolius chlorosteus</i>	Boulenger, 1915	86,033
Anura	Hyperoliidae	<i>Hyperolius concolor</i>	(Hallowell, 1844)	909,771
Anura	Hyperoliidae	<i>Hyperolius fusciventris</i>	Peters, 1876	122,323
Anura	Hyperoliidae	<i>Hyperolius guttulatus</i>	Günther, 1858	579,249
Anura	Hyperoliidae	<i>Hyperolius igbettensis</i>	Schiøtz, 1963	1,096,169
Anura	Hyperoliidae	<i>Hyperolius koehleri</i>	(Mertens, 1940)	90,459
Anura	Hyperoliidae	<i>Hyperolius lamottei</i>	Laurent, 1958	404,450
Anura	Hyperoliidae	<i>Hyperolius lamtoensis</i>	Schiøtz, 1967*	535
Anura	Hyperoliidae	<i>Hyperolius laurenti</i>	Schiøtz, 1967	67,629
Anura	Hyperoliidae	<i>Hyperolius nienokouensis</i>	Rödel, 1998	2,847
Anura	Hyperoliidae	<i>Hyperolius nimbae</i>	Laurent, 1958	8,197
Anura	Hyperoliidae	<i>Hyperolius nitidulus</i>	Peters, 1875	1,716,211
Anura	Hyperoliidae	<i>Hyperolius occidentalis</i>	Schiøtz, 1967	208,233
Anura	Hyperoliidae	<i>Hyperolius ocellatus</i>	Günther, 1858	1,915,390
Anura	Hyperoliidae	<i>Hyperolius picturatus</i>	Peters, 1875	328,894
Anura	Hyperoliidae	<i>Hyperolius riggenbachi</i>	(Nieden, 1910)	70,410
Anura	Hyperoliidae	<i>Hyperolius soror</i>	(Chabanaud, 1921)	154,956
Anura	Hyperoliidae	<i>Hyperolius spatzi</i>	Ahl, 1931	286,523
Anura	Hyperoliidae	<i>Hyperolius sylvaticus</i>	Schiøtz, 1967	603,626
Anura	Hyperoliidae	<i>Hyperolius torrentis</i>	Schiøtz, 1967	9,759
Anura	Hyperoliidae	<i>Hyperolius tuberculatus</i>	(Mocquard, 1897)	1,860,763
Anura	Hyperoliidae	<i>Hyperolius viridigulosus</i>	Schiøtz, 1967	121,681
Anura	Hyperoliidae	<i>Hyperolius zonatus</i>	Laurent, 1958	165,347
Anura	Hyperoliidae	<i>Kassina arboricola</i>	Perret, 1985	135,338
Anura	Hyperoliidae	<i>Kassina cassinoides</i>	(Boulenger, 1903)	1,334,063
Anura	Hyperoliidae	<i>Kassina cochranee</i>	(Loveridge, 1941)	315,972
Anura	Hyperoliidae	<i>Kassina fusca</i>	Schiøtz, 1967	1,041,832
Anura	Hyperoliidae	<i>Kassina lamottei</i>	Schiøtz, 1967	67,414
Anura	Hyperoliidae	<i>Kassina schioetzi</i>	Rödel <i>et al.</i> , 2002	136,347
Anura	Hyperoliidae	<i>Kassina senegalensis</i>	(Duméril & Bibron, 1841)	9,714,724
Anura	Hyperoliidae	<i>Morerella cyanophthalma</i>	Rödel <i>et al.</i> , 2009	25
Anura	Hyperoliidae	<i>Opisthophyllax immaculatus</i>	(Boulenger, 1903)	342,650
Anura	Hyperoliidae	<i>Phlyctimantis boulengeri</i>	Perret, 1986	242,452



Anura	Odontobatrachidae	<i>Odontobatrachus natator</i> 1	Boulenger, 1905*	102,918
Anura	Odontobatrachidae	<i>Odontobatrachus natator</i> 2	Boulenger, 1905*	4,200
Anura	Odontobatrachidae	<i>Odontobatrachus natator</i> 3	Boulenger, 1905*	43,837
Anura	Odontobatrachidae	<i>Odontobatrachus natator</i> 4	Boulenger, 1905*	4,053
Anura	Odontobatrachidae	<i>Odontobatrachus natator</i> 5	Boulenger, 1905*	5,708
Anura	Petropedetidae	<i>Petropedetes cameronensis</i>	Reichenow, 1874	41,269
Anura	Petropedetidae	<i>Petropedetes parkeri</i>	Amiet, 1983	89,346
Anura	Phrynobatrachidae	<i>Phrynobatrachus africanus</i>	(Hallowell, 1858)	294,922
Anura	Phrynobatrachidae	<i>Phrynobatrachus alleni</i>	Parker, 1936	237,649
Anura	Phrynobatrachidae	<i>Phrynobatrachus annulatus</i>	Perret, 1966	121,490
Anura	Phrynobatrachidae	<i>Phrynobatrachus auritus</i>	Boulenger, 1900	898,668
Anura	Phrynobatrachidae	<i>Phrynobatrachus batesii</i>	(Boulenger, 1906)	838,638
Anura	Phrynobatrachidae	<i>Phrynobatrachus calcaratus</i>	(Peters, 1863)	922,497
Anura	Phrynobatrachidae	<i>Phrynobatrachus cricogaster</i>	Perret, 1957	33,767
Anura	Phrynobatrachidae	<i>Phrynobatrachus francisci</i>	Boulenger, 1912	1,679,305
Anura	Phrynobatrachidae	<i>Phrynobatrachus fraterculus</i>	(Chabanaud, 1921)	144,104
Anura	Phrynobatrachidae	<i>Phrynobatrachus ghanensis</i>	Schiøtz, 1964	34,351
Anura	Phrynobatrachidae	<i>Phrynobatrachus guineensis</i>	Guibé & Lamotte, 1962	153,808
Anura	Phrynobatrachidae	<i>Phrynobatrachus gutturosus</i>	(Chabanaud, 1921)	859,425
Anura	Phrynobatrachidae	<i>Phrynobatrachus intermedius</i>	Rödel <i>et al.</i> , 2009	336
Anura	Phrynobatrachidae	<i>Phrynobatrachus latifrons</i>	Ahl, 1924	1,255,058
Anura	Phrynobatrachidae	<i>Phrynobatrachus liberiensis</i>	Barbour & Loveridge, 1927	128,903
Anura	Phrynobatrachidae	<i>Phrynobatrachus natalensis</i>	(Smith, 1849)	8,832,188
Anura	Phrynobatrachidae	<i>Phrynobatrachus phyllophilus</i>	Rödel & Ernst, 2002	152,748
Anura	Phrynobatrachidae	<i>Phrynobatrachus plicatus</i>	(Günther, 1858)	269,218
Anura	Phrynobatrachidae	<i>Phrynobatrachus steindachneri</i>	Nieden, 1910	50,251
Anura	Phrynobatrachidae	<i>Phrynobatrachus tokba</i>	(Chabanaud, 1921)	287,989
Anura	Phrynobatrachidae	<i>Phrynobatrachus villiersi</i>	Guibé, 1959	248,686
Anura	Phrynobatrachidae	<i>Phrynobatrachus werneri</i>	(Nieden, 1910)	48,126
Anura	Phrynobatrachidae	<i>Phrynomantis microps</i>	Peters, 1875	2,161,348
Anura	Pipidae	<i>Hymenochirus boettgeri</i>	(Tornier, 1896)	2,225,505
Anura	Pipidae	<i>Pseudhymenochirus merlini</i>	Chabanaud, 1920	165,890
Anura	Pipidae	<i>Xenopus laevis</i>	(Daudin, 1802)	4,879,094
Anura	Pipidae	<i>Xenopus muelleri</i>	(Peters, 1844)	5,585,683
Anura	Pipidae	<i>Xenopus tropicalis</i>	(Gray, 1864)	1,077,770
Anura	Ptychadenidae	<i>Hildebrandtia ornata</i>	(Peters, 1878)	11,153,390
Anura	Ptychadenidae	<i>Ptychadena aequiplicata</i> 1	(Werner, 1898)*	650,864
Anura	Ptychadenidae	<i>Ptychadena aequiplicata</i> 2	(Werner, 1898)*	97,804
Anura	Ptychadenidae	<i>Ptychadena aequiplicata</i> 3	(Werner, 1898)*	187,240
Anura	Ptychadenidae	<i>Ptychadena bibroni</i>	(Hallowell, 1845)	1,908,248
Anura	Ptychadenidae	<i>Ptychadena longirostris</i>	(Peters, 1870)	445,784
Anura	Ptychadenidae	<i>Ptychadena mascareniensis</i> complex	(Duméril & Bibron, 1841)	7,835,548
Anura	Ptychadenidae	<i>Ptychadena oxyrhynchus</i>	(Smith, 1849)	7,747,981
Anura	Ptychadenidae	<i>Ptychadena pujoli</i>	Lamotte & Ohler, 1997	780,550
Anura	Ptychadenidae	<i>Ptychadena pumilio</i>	(Boulenger, 1920)	2,330,399
Anura	Ptychadenidae	<i>Ptychadena retropunctata</i>	(Angel, 1949)	84,917
Anura	Ptychadenidae	<i>Ptychadena schillukorum</i>	(Werner, 1908)	7,821,618
Anura	Ptychadenidae	<i>Ptychadena submascareniensis</i>	(Guibé & Lamotte, 1953)	88,219
Anura	Ptychadenidae	<i>Ptychadena superciliaris</i>	(Günther, 1858)	382,255
Anura	Ptychadenidae	<i>Ptychadena tellinii</i>	(Peracca, 1904)	3,093,301
Anura	Ptychadenidae	<i>Ptychadena tournieri</i>	(Guibé & Lamotte, 1955)	1,010,511
Anura	Ptychadenidae	<i>Ptychadena trinodis</i>	(Boettger, 1881)	3,492,962
Anura	Pyxicephalidae	<i>Aubria occidentalis</i>	Perret, 1995	574,508
Anura	Pyxicephalidae	<i>Pyxicephalus edulis</i>	Peters, 1854	2,153,009
Anura	Pyxicephalidae	<i>Tomopterna</i> sp. (<i>cryptotis</i>)	(Boulenger, 1907)*	475,838
Anura	Ranidae	<i>Hylarana albolabris</i> complex	(Hallowell, 1856)	2,322,242
Anura	Ranidae	<i>Hylarana asperrima</i>	Perret, 1977	26,222
Anura	Ranidae	<i>Hylarana galamensis</i>	(Duméril & Bibron, 1841)	5,024,844
Anura	Ranidae	<i>Hylarana occidentalis</i>	(Perret, 1960)	89,810
Anura	Rhacophoridae	<i>Chiromantis rufescens</i>	(Günther, 1869)	1,126,242



Gymnophiona	Dermophiidae	<i>Geotrypetes</i> sp. (<i>seraphini</i>)	(Duméril, 1859)	650,678
Gymnophiona	Herpidae	<i>Herpele squalostoma</i>	(Stutchbury, 1836)	509,233



8 List of Publications

8.1 Publications “peer reviewed”

- Rödel, M.-O., Emmrich, M., Penner, J., Schmitz, A. & Barej, M.F. (2014). The taxonomic status of two West African *Leptopelis* species: *L. macrotis* Schiøtz, 1967 and *L. spiritusnoctis* Rödel, 2007 (Amphibia: Anura: Arthroleptidae). *Zoosystematics & Evolution* 90: 21-31.
- Hoffmann, A., Penner, J., Vohland, K., Cramer, W., Doubleday, W., Henle, K., Köljal, U., Kühn, I., Kunin, W.E., Negro, J.J., Penev, L., Rodríguez, C., Saarenmaa, H., Schmeller, D.S., Stoev, P., Sutherland, W.J., Ó Tuama, É., Wetzel, F.T. & Häuser, C.L. (2014). Improved access to integrated biodiversity data for science, practice, and policy - the European Biodiversity Observation Network (EU BON). *Nature Conservation* 6: 49-65.
- Kouamé, N.G., Adepo-Gourène, A.B., Konan, J.C.B.Y.N., Emmrich, M., Penner, J. & Rödel, M.-O. (2014). Second record of *Hyperolius laurenti* Schiøtz, 1967 (Anura: Hyperoliidae) in south-eastern Ivory Coast, with observations on the species' variability, call characteristics and habitat. *Herpetology Notes* 7: 59-65.
- Barej, M.F., Rödel, M.-O., Loader, S.P., Menegon, M., Gonwouo, N.L., Penner, J., Gvoždík, V., Günther, R., Bell, R.C., Nagel, P. & Schmitz, A. (in press). Light shines through the spindrift – Phylogeny of African torrent frogs (Amphibia, Anura, Petropedetidae). *Molecular Phylogenetics & Evolution*.
- Penner, J., Gonwouo, N.L. & Rödel, M.-O. (2013). Second record of the West African hairy bush viper *Atheris hirsuta* Ernst & Rödel, 2002 (Serpentes: Viperidae). *Zootaxa* 3694: 196–200.
- Doherty-Bone, T.M., Gonwouo N.L., Hirschfeld, M., Ohst, T., Weldon, C., Perkins, M., Kouete, M.T., Browne, R.K., Loader, S.P., Gower, D.J., Wilkinson, M.W., Rödel, M.-O., Penner, J., Barej, M.F., Schmitz, A., Plötner, J. & Cunningham, A.A. (2013). *Batrachochytrium dendrobatidis* in amphibians of Cameroon, including first records for caecilians. *Diseases of Aquatic Organisms* 102: 187–194.
- Penner, J., Adum, G.B., McElroy, M.T., Doherty-Bone, T., Hirschfeld, M., Sandberger, L., Weldon, C., Cunningham, A.A., Ohst, T., Wombwell, E., Portik, D.M., Reid, D., Hillers, H., Ofori-Boateng, C., Oduro, W., Plötner, J., Ohler, A., Leaché, A.D. & Rödel, M.-O. (2013). West Africa - A Safe Haven for Frogs? A Sub-Continental Assessment of the Chytrid Fungus (*Batrachochytrium dendrobatidis*). *PLOS ONE* 8: e56236
- Rödel, M.-O., Barej, M.F., Hillers, A., Leaché, A., Kouamé G.N., Ofori Boaten, C., Assemian, N.E., Tohé, B., Penner, J., Hirschfeld, M., Doumbia, J., Gonwouo, L.N., Nopper, J., Brede, C., Diaz, R., Fujita, M.K., Gil, M., Segniagbeto, G.H., Ernst, R. & Sandberger, L. (2012). The genus *Astylosternus* in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae). *Zootaxa* 3245: 1-29.
- Penner, J., Wegmann, M., Hillers, A., Schmidt, M. & Rödel, M.-O. (2011). A hotspot revisited – a biogeographical analysis of West African amphibians. *Diversity & Distributions* 17: 1077-1088.
- Rödel, M.-O., Sandberger, L., Penner, J., Mané, Y. & Hillers, A. (2010). The taxonomic status of *Hyperolius spatzi* Ahl, 1931 and *Hyperolius nitidulus* Peters, 1875 (Amphibia: Anura: Hyperoliidae). *Bonn zoological Bulletin* 57: 177-188.
- Rödel, M.-O., Ofori-Boateng, C., Penner, J. & Hillers, A. (2009). A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa. *Zootaxa* 1970: 52-62.
- Penner, J., Fruteau, C., Range, F. & M.-O. Rödel (2008). Finding a needle in a haystack - new methods of locating and working with Gaboon Vipers. *Herpetological Review* 39: 310-314.
- Rödel, M.-O., Brede, C., Schiefenhövel, P., Penner, J., Sinsin, B. & Nago, S.G.A. (2007). The amphibians of the Lokoli Forest, a permanently inundated rainforest in the Dahomey Gap, Benin. *Salamandra* 43: 231-238.

8.2 Book chapters

- Penner, J., Rödel, M.-O. & Mey, W. (2011). Forschungen zur Biodiversität in Afrika - Die Beiträge des Museums für Naturkunde für das BIOTA-Projekt. 278-281. In: Damaschun, F., Hackethal, S., Landsberg, H. & Leinfelder, R. (Eds.). *Klasse, Ordnung, Art. 200 Jahre Museum für Naturkunde. Basiliken-Presse im Verlag Natur & Text, Rangsdorf.*
- Penner, J., Adeba, P.J., Hillers, A., Nago, S.G.N. & Rödel, M.-O. (2010). Amphibiens de l'Afrique de l'Ouest / West African amphibians. 102-107. In: Sinsin, B. & Kampmann, D. (Eds.). *Atlas de la biodiversité de l'Afrique de l'Ouest, / Biodiversity atlas of West Africa / Volume I / II / III: Bénin / Burkina Faso / Côte d'Ivoire. Cotonou / Ouagadougou / Abidjan & Frankfurt/M.*
- Rödel, M.-O., Adeba, P.J., Kouamé, G.N. & Penner, J. (2010). 5.10 Les amphibiens / Amphibians. 218-222. In: Konaté, S. & Kampmann, D. (Eds.). *Atlas de la biodiversité de l'Afrique de l'Ouest, / Biodiversity atlas of West Africa, Tome / Volume III: Côte d'Ivoire. Abidjan & Frankfurt/M.*
- Nago, S.G.A., Penner, J., Sinsin, B. & Rödel, M.-O. (2010). Les amphibiens 7.5 Diversité des amphibiens au Bénin: situation actuelle et futur / Amphibian diversity in Benin: current stage and outlook. 394-397. In: Sinsin, B. &



Kampmann, D. (Eds.). Atlas de la biodiversité de l'Afrique de l'Ouest, / Biodiversity atlas of West Africa, Tome / Volume I: Bénin. Cotonou & Frankfurt/M.

Rödel, M.-O., Adeba, P.J., Ernst, R., Hillers, A., Nago, S.G.A., Penner, J. & Wegmann, M. (2008). Threatened islands of amphibian diversity in West Africa. 62-63. In: Stuart, S., M. Hoffmann, J. Chanson, N. Cox, R. Berridge, P. Ramani & B. Young (Eds.). Threatened amphibians of the world. IUCN Gland, Switzerland & Conservation International, Arlington, USA.

Penner, J. & Rödel, M.-O. (2007). Amphibians and Reptiles of Lokutu. 37-41. In: Butynski, T.M. & J. McCullough (Eds.). A Rapid Biological Assessment of Lokutu, Democratic Republic of Congo. RAP Bulletin of Biological Assessment 46. Conservation International, Arlington, USA.

Weinmann, K., Beck, C., Madl, R., Penner, J., Sound, P., Wollesen, R. & Joger, U. (2004). Zur Ökologie und Raum-Zeit-Einbindung einer Kreuzotterpopulation (*Vipera berus* [L.] im Hessischen Spessart. 197-212. In: Joger, U. & Wollesen, R. (Eds.). Verbreitung, Ökologie und Schutz der Kreuzotter (*Vipera berus* [Linnaeus, 1758]). Mertensiella 15.

8.3 Other publications

Penner, J. (2012). Buchbesprechung: Aldridge, R.D. & Sever, D.M. [Eds.] (2011). Reproductive Biology and Phylogeny of Snakes. Sauria 34: 16-18.

Penner, J., Toudonou, C.A.S., Sinsin, B. & Rödel, M.-O. (2008). Die Nutzung von Schlangen und die damit verbundenen ökonomischen und ökologischen Folgen - das Beispiel des Königspythons in Westafrika. Draco 35: 64-68.

Rödel, M.-O., Penner, J. & Nago, S.G.A. (2007). Bericht von der 12. Tagung der Arbeitsgruppe „Afrikanische Amphibien“ und dem Pendjari Amphibien Workshop in Benin, Westafrika. Elaphe 15: 19-22.

Fuchs, J., Grohmann, C., Rödel, M.-O. & Penner, J. (2006). Ökologische Untersuchungen an Reptilien einer Dornbuschsavanne in Zentralnamibia - Unwägbarkeiten der Freilandforschung. Elaphe 14: 55-60.

Rödel, M.-O., Adeba, P.J., Nago, S.G.A., Penner, J., Sinsin, B., Veith, M. & Linsenmair, K.E. (2005). Establishing of an amphibian bio-indicator system and capacity building in West Africa, as basis for a sustainable bio-diversity management. BIOLOG, Biodiversity and Global Change Status Report 2005, Federal Ministry of Education and Research, Bonn: 128-129.

Penner, J. (2001). Der größte Schlangenzoo Lateinamerikas - ein Praktikum im "World of Snakes", Grecia, Costa Rica. Elaphe 9: 81-85.

8.4 Presentations

Penner, J. (2013). Lightning talk "What should a flora/fauna/mycota of the future be able to do for me?" pro-iBiosphere Workshop, 21.-23. May 2013, Berlin.

Penner, J., Augustin, M. & Rödel, M.-O. (2013). Detecting biogeographical barriers - testing and putting beta diversity on a map. HPI Future SOC Lab Day, 10. April 2013, Potsdam.

Häuser, C. & Hoffmann, A., Pinho, C., Müller, M., Vohland, K., Glöckler, F., Kroupa, A., Penner, J. (2013). Delivering integrated biodiversity information – perspectives from EU BON. EU BON Symposium, 11.-12. Februar 2013, Berlin.

Penner, J. & Barej, M.F.B. (2012). Biogeographical patterns of West African amphibians - searching for causes in time and space. World Congress of Herpetology 7, 8.-14. August 2012, Vancouver, Kanada.

Greenbaum, E., Conkey, N., Pramuk, J., Carr, J., Rödel, M.-O., Penner, J. (2012). Systematics of Congo Basin True Toads (Anura: Bufonidae: *Amietophrynus*) Reveals Widespread Cryptic Speciation. World Congress of Herpetology 7, 8.-14. August 2012, Vancouver, Kanada.

Penner, J., Adum, G.B., McElroy, M.T., Doherty-Bone, T., Hirschfeld, M., Sandberger, L., Weldon, C., Cunningham, A.A., Ohst, T., Wombwell, E., Portik, D.M., Reid, D., Hillers, A., Ofori-Boateng, O., Oduro, W., Plötner, J., Ohler, A., Leaché, A.D. & Rödel, M.-O. (2012). A last resort? Search for *Bd* in Western Africa. 15th African Amphibian Working Group Meeting, 28.-31. Mai, Trient, Italien.

Penner, J. & Rödel, M.-O. (2010). Biogeography of West African amphibians - insights from extrapolations & modelling. 14th African Amphibian Working Group Meeting, 1.-3. Juni, Nordhoek, Südafrika.

Penner, J., Hillers, A., Herkt, M., Fahr, J. & Rödel M.-O. (2009). An amphibian hotspot revisited - does a finer scale give new answers? Jahrestagung der GTÖ & ATBC „Impacts of Global Change on Tropical Ecosystems - cross-cutting the Abiotic, Biotic and Human Spheres“, 27.-30. Juli, Marburg.

Penner, J., Hillers, A., Herkt, M., Fahr, J. & Rödel M.-O. (2009). An amphibian hotspot revisited - does a finer scale give new answers? Jahrestagung der SCB „Conservation: Harmony for Nature and Society“, 11.-16. Juli, Peking, China.



- Penner, J. & Rödel, M.-O. (2009). Nischen- und Habitatmodellierung - Möglichkeiten eines Werkzeuges der ökologischen Forschung. Ecology & Energetics - Innovative concepts and methods in field biology, 4. April, Hamburg.
- Penner, J. & Rödel, M.-O. (2008). Nischen- und Habitatmodellierung - Möglichkeiten eines Werkzeuges der ökologischen Forschung. Methoden der Feldherpetologie, 7.-9. November, Bonn.
- García Márquez, J.R., Barnikel, G., Barthlott, W., Da, S., Dressler, S., Fahr, J., Herkt, M., Janssen, T., Kalko, E., König, K., Landmann, T., Linsenmair, K.E., Penner, J., Rödel, M.-O., Schmidt, M., Schmidt, M., Sommer, J.H., Thiombiano, A., Wegmann, M. & Zizka, G. (2008). Cross-taxon patterns of biodiversity, land cover, and protected areas in West Africa. Biodiversity of Africa - Observation and Sustainable Management for our Future! 29. September - 3. Oktober, Spier, Südafrika.
- Fahr, J., Barnikel, G., García-Márquez, J.R., Hillers, A., Kalko, E., Penner, J., Schmidt, M., Sommer, J.H., Wegmann, M. & M.-O. Rödel (2008). Mountains, mining, and threatened species - a deadly cocktail for the long-term conservation of a global biodiversity hotspot. Biodiversity of Africa - Observation and Sustainable Management for our Future! 29. September - 3 Oktober, Spier, Südafrika.
- Herkt, KMB, Barnikel, G., Fahr, J., Finckh, M., García Marquez, J.R., König, K., Oldeland, J., Penner, J., Rödel, M.-O., Schmidt, M., Sommer, J.H. & Wegmann M. (2008). Opportunities, challenges and limitations of species distribution models: Implications for decision-making in support of biodiversity conservation and sustainable land use. Biodiversity of Africa - Observation and Sustainable Management for our Future! 29. September - 3. Oktober, Spier, Südafrika.
- Wegmann, M., Magidi, J., Lung, T., Schaab, G., Krug, C., Knight, J., Sommer, J.H., Sabellek, K., Fahr, J., Herkt, M., Barnikel, G., Penner, J., Rödel, M.-O., Keil, M., Landmann, T. & Schmidt, M. (2008). Spatial pattern analysis across Africa for a better understanding of biodiversity patterns using remote sensing. Biodiversity of Africa - Observation and Sustainable Management for our Future! 29. September - 3. Oktober, Spier, Südafrika.
- Penner, J. & Rödel, M.-O. (2008). Threatened amphibians in Western Africa - spatial analyses with different data sets. 1st PhD Student Symposium am Institut für Zoo & Wildtierforschung, 10.-12. September, Berlin.
- Penner, J., J. Fahr, M. Wegmann, M. Schmidt & Rödel, M.-O. (2008). Bedrohte Amphibien in Westafrika - Wo und warum? DGHT Jahrestagung 3.-7. September, Potsdam.
- Fahr, J., Barnikel, G., Hillers, A., Penner, J., Wegmann, M., Kalko, E. & Rödel, M.-O. (2008). Mountains, mining, and threatened species - a deadly cocktail for the long-term conservation of a global biodiversity hotspot. Jahrestagung der ATBC „Past and recent history of tropical ecosystems: cross- continental comparisons and lessons for the future“, 9.-13. Juni, Paramaribo, Surinam.
- Toudonou A.S.C., Penner, J., Rödel, M.-O. & Sinsin, B. (2007). Utilisation and Conservation of Royal Pythons. BIOTA West Workshop, 7.-11. Oktober, Natitingou, Benin.
- Penner J., Dehling, M., Joger, U., Zitzmann, A. & Rödel, M.-O. (2007). Ten years of adder (*Vipera b. berus*) research – results and conservation recommendations. 2nd Biology of the Vipers Conference, 24.-27. September, Porto, Portugal.
- Penner J., Wegmann, M., Konrad, T., Hillers, A., Schmidt, M. & Rödel, M.-O. (2007). Amphibians and their conservation in western Africa. 14th European Congress of Herpetology, 19.-23. September, Porto, Portugal.
- Wegmann, M., Gros, A., Schmidt, M., Colditz, R., Fahr, J., Penner, J., Rödel, M.-O., Linsenmair, K.-E. & Dech, S. (2007). Species in a dynamic landscape – a spatio-temporal analysis using MODIS time-series. - ISRSE 2007. 32nd International Symposium on Remote Sensing of Environment: "Sustainable Development through Global Earth Observations", 25. June, San Jose, Costa Rica.
- Fahr, J., Barnickel, G., Hillers, A., Penner, J., Wegmann, M., Kalko, E. & Rödel, M.-O. (2007). Mountains, mining, and threatened species - a deadly cocktail for the long-term conservation of a global biodiversity hotspot. - 20. Jahrestagung der GTÖ „Tropical Diversity in the Anthropocene“, 21.-25. Februar, Bonn.
- Wegmann, M., Colditz, R.R., Fahr, J., Landmann, T., Linsenmair, K.E., Penner, J., Rödel, M.-O., Schmidt, M., Sommer, H., & Dech, S. (2006). Spatio-temporal analysis of African landscapes for biodiversity research. - 6. International Conference of the African Association of Remote Sensing of the Environment, 30. Oct.-2. Nov. Cairo, Egypt.
- Yao, N. A., Schmidt, M., Landmann, T., Wegmann, M., Konaté, S., Penner, J., Rödel, M.-O., Fahr, J. & Linsenmair, K. E. (2006) Satellite derived spatial and temporal distribution of fire activity in subsahelian West Africa. - 6. International Conference of the African Association of Remote Sensing of the Environment, 30. Oct.-2. Nov. Cairo, Egypt.
- Penner, J., Wegmann, M., Schmidt, M. & Rödel, M.-O. (2006). Conservation priorities of herps in western Africa. - 12th African Amphibians Working Group Meeting, 14.-17. August, Abomey, Benin.
- Penner, J. & Rödel, M.-O. (2005). Macroecology of Herps in Western Africa. BIOTA West Workshop, 3.-7. Oktober, Natitingou, Benin.
- Penner, J., Kroiß, J., Glos, J. & Rödel, M.-O. (2005). The influence of fragmentation and selective logging on reptile communities. - 5th World Congress of Herpetology, 19.-24. Juni, Stellenbosch, Südafrika.



Penner, J., Kroiß, J., Glos, J. & Rödel, M.-O. (2004). Reptiliengemeinschaften entlang eines Habitat- & Störungsgradienten in einem Trockenwald in West Madagaskar. - DGHT Jahrestagung, 23.-26. September, Norderstedt.

Penner, J., Kroiß, J., Glos, J. & Rödel, M.-O. (2004). Ein Vergleich der Reptiliengemeinschaften im Kirindy. - Kirindy-Symposium, 18. Juni, Göttingen.

Weinmann, K., Beck, C., Penner, J., Sound, P., Wollesen, R. & Joger, U. (2001). Ökologie und Raum-Zeit-Einbindung einer Kreuzotterpopulation im hessischen Spessart. - DGHT AG Feldherpetologie Tagung, 22.-24. November, Darmstadt.

Weinmann, K., Wollesen, R. & Penner, J. (2001). Die Kreuzotter im Spessart - ein Artenschutzprojekt der Arbeitsgemeinschaft Amphibien und Reptilienschutz in Hessen e.V. AGAR. Tagung der Arbeitsgemeinschaft Amphibien- & Reptilienschutz in Hessen e.V. (AGAR), 12. Mai, Bad Schlangenbad.

8.5 Poster

Penner, J., Hirschfeld, M., Doherty-Bone, T., McElroy, M.T., Ohst, T., Sandberger, L., Plötner, J., Weldon, C., Leaché, A. & Rödel, M.-O. (2013). The amphibian chytrid fungus *Batrachochytrium dendrobatidis* - an African perspective. 2nd International Conference on Biodiversity and the UN Millennium Development Goals, Challenges for Research & Action, 16.-18. April 2013, Berlin.

Häuser, C., Hoffmann, A., Vohland, K. & Penner, J. (2013). EU BON - Building the European Biodiversity Observation Network. 7. Jahrestagung der „Specialist Group on Macroecology of the Ecological Society of Germany, Austria and Switzerland (GfÖ)“, 13.-15. März, Göttingen. 2nd International Conference on Biodiversity and the UN Millennium Development Goals, Challenges for Research & Action, 16.-18. April 2013, Berlin.

Häuser, C., Hoffmann, A., Vohland, K. & Penner, J. (2013). Museum für Naturkunde. EU BON Kickoff Meeting, 13.-15. Februar. Berlin.

Nago, S.G.A., Penner, J., Sinsin, B. & Rödel, M.-O. (2007). Savannah amphibians along a disturbance gradient - first results from the Pendjari region, Benin. 20. Jahrestagung der GTÖ „Tropical Diversity in the Anthropocene“, 21.-25. Februar, Bonn.

Gonwouo, N.L., Penner, J. & Rödel, M.-O. (2007). Influence of altitude and anthropogenic alteration on amphibians - insights from Mt Manengouba, Cameroon. 20. Jahrestagung der GTÖ „Tropical Diversity in the Anthropocene“, 21.-25. Februar, Bonn.

Adeba, P.J., Penner, J., Kouassi, P. & Rödel, M.-O. (2007). Amphibian communities in forest islands - a case study from the Côte d'Ivoire. 20. Jahrestagung der GTÖ „Tropical Diversity in the Anthropocene“, 21.-25. Februar, Bonn.

Penner, J., Wegmann, M. & Rödel, M.-O. (2006). Distribution of Herp's in Western Africa - Call for Your Contribution!!! 18. World Meeting of the Crocodile Specialist Group, IUCN Species Survival Commission, 19.-24. Juni, Montélimar, Frankreich.

Penner, J., Wegmann, M. & Rödel, M.-O. (2006). Conservation of amphibians and reptiles within the interdisciplinary research project of BIOTA West. Student Conference for Conservation Science, 28.-30. März, Cambridge, UK.

Nago, S.G.A., Penner, J., Adeba, P.J., Sinsin, B., Kouassi, P., Gourene, G., Linsenmair, K.E. & Rödel, M.-O. (2005). Amphibians as a bio-indicator system for a sustainable bio-diversity management. Outlook to final phase. 19. Jahrestagung der GTÖ „Connecting microbes, plants, animals and human impact“, 21.-24. Februar, Kaiserslautern.

Adeba, P.J., Nago, S.G.A., Penner, J., Ernst, R., Hillers, A., Veith, M., Kouassi, P., Sinsin, B., Gourene, G., Linsenmair, K.E. & Rödel, M.-O. (2005). Establishing of an amphibian bio-indicator system and capacity building in West Africa, as basis for a sustainable bio-diversity management. Past and present work. 19. Jahrestagung der GTÖ „Connecting microbes, plants, animals and human impact“, 21.-24. Februar, Kaiserslautern.

Nago, S.G.A., Penner, J., Adeba, P.J., Sinsin, B., Kouassi, P., Gourene, G., Linsenmair, K.E. & Rödel, M.-O. (2005). Amphibians as a bio-indicator system for a sustainable bio-diversity management. Outlook to final phase. BIOLOG Status Seminar, 25.-27. November, Würzburg.

Adeba, P.J., Nago, S.G.A., Penner, J., Ernst, R., Hillers, A., Veith, M., Kouassi, P., Sinsin, B., Gourene, G., Linsenmair, K.E. & Rödel, M.-O. (2005). Establishing of an amphibian bio-indicator system and capacity building in West Africa, as basis for a sustainable bio-diversity management. Past and present work. BIOLOG Status Seminar, 25.-27. November, Würzburg.

Wegmann, M., Schmidt, M., Schramm, M., Yao, N., Keil, M., Goetze, D., Rödel, M.-O., Penner, J., Fahr, J., Barnikel, G. & König, K. (2005). ... to Biodiversity. Surface parameter as indicator for biological diversity. BIOLOG Status Seminar, 25.-27. November, Würzburg.

Cheikh, A.T.A., Djossa, B., Fahr, F., Hahn-Hadjali, K., Kaiser, D., Kalko, E., König, K., Korb, J., Lange, U., Linsenmair, K.E., Moritz, T., Nago, S.G.A., Penner, J., Rödel, M.-O., Runge, J., Schmidt, M., Sinsin, B., Szarzynski, J., Tehou, A., Tiomoko, A.D. & Wegmann, M. (2005). The Pendjari National Park in Benin - A centre of research and co-operation in the framework of BIOTA West. BIOLOG Status Seminar, 25.-27. November, Würzburg.



Barthlott, W., Fahr, J., Hahn-Hadjali, K., Kalko, E., Küper, W., Penner, J., Rödel, M.-O., Sommer, H., Schmidt, M., Szarzynski, J., Thiombiano A. & Wegmann M. (2005). Broad-scale diversity patterns, priority setting and conservation strategies: Analytical and methodological approaches for West Africa. BIOLOG Status Seminar, 25.-27. November, Würzburg.

Penner, J., Kroiß, J., Glos, J. & Rödel, M.-O. (2004). Reptile community composition along humidity and disturbance gradients in the Kirindy dry forest, western Madagascar. African Biodiversity, molecules, organisms, ecosystems, 5th International Symposium on Tropical Biology, 2.-6. Mai, Bonn.

Penner, J., Kroiß, J., Glos, J. & Rödel, M.-O. (2003). Reptile community composition along humidity and disturbance gradients in the Kirindy dry forest, western Madagascar. Tropical savannas & seasonally dry forests. Ecology, environment and development, 15.-20. September, Edinburgh, UK.



Contributions to the different chapters with the following abbreviations: c = contributed; l = lead;
* = lead for the ENM data collection.

	3.1.1	3.1.2	3.1.3	3.2	3.3	3.4.1	3.4.2
conceived idea & research				l	l	l	l
data collection	c	c	c	l	l*	l	l
data analyses	c	c	c	l	l	l	l
writing of manuscript	c	c	c	l	l	l	l





9 Statement / Erklärung

Herewith I state that I accomplished the present study independently. I did not use any other resources or references than cited in here.

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Berlin, 19.12.2013